Modern Developments *in* Animal Breeding

If then Socrates we find ourselves unable to make our discourse in every way wholly consistent and exact you must not be surprised Nay, we must be well content if we can provide an account not less likely than another, we must remember that I who speak and you who are my audience are but men and should be satisfied to ask for no more than the likely story

Modern Developments *in* Animal Breeding

By

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FOREWORD

The scientific revolution, viewed by Bernal some twenty-five years ago as a twentieth century parallel to the industrial revolution, has since the war assumed proportions unprecedented in human history. The rate of change and magnitude of its effects are altering the daily life and attitudes of most of mankind. In turn, the social changes brought about, and other effects such as population pressure, influence the workings of science. For one thing, they affect scientific goals and for another, they modify the ways in which scientific information is spread and the political institutions through which it is exploited. As far as biology, and more specifically genetics, is concerned, there has been within the last few decades such progress, such growing power over nature, as to warrant a determined effort by all who have an interest in the future pattern of society to consider where this technical progress is taking us. The startling achievements of the physical and chemical sciences should not be allowed to obscure the fact that biology also brings its gifts which if properly used can improve the lot of man. Given the prospect of directed control by man over the evolution of his own species and of his agricultural crops and plants, it is surely wise to consider who is exercising this power.

Agriculture, in common with other industries, is experiencing an intensification which shows itself in the rising output of a worker and the falling number of individual enterprises. It is also to be seen in the trend towards integration. Livestock production is not immune to these changes and its positive response to the economic advantages of large businesses has created a need for a new and vigorous technology. While the structure of animal production is being modified, its genetic efficiency is a matter of deep concern and, at least in some circumstances, a factor of sufficient importance to alter the outcome of the process. It is our hope that this book will help to ensure that the urgent need for more animal protein will be communicated to those who are influential to any degree in increasing the speed at which new and better livestock can be developed. To this end a survey of the issues faced in the organisation and carrying out of animal improvement by state as well as by private and quasi-private agencies is opportune, for surprisingly enough this task has not hitherto been undertaken. Despite the abundance of publications on animal production, there is a marked lack of discussion about the interplay between the technology and the economics of breeding. Although the repercussions of such developments as artificial insemination and performance testing on the structure of agricultural

industries have been common knowledge for many years, recent textbooks on animal production and breeding have little or no mention of them. Students, to the extent that they have to depend on literature, cannot readily consider what may be learned from the poultry industry that is valid for larger animals, nor, indeed, are they given a hint that the logic of performance testing, to say nothing of the pressure on food supplies, may require modifications in the current systems of breeding improved livestock.

There are several restraints circumscribing both the intent and the execution of this volume which are due to the limitations of our training and experience. Economics, political theory, sociology, and psychology are all woven into the fabric of the issues to be examined. Since we cannot claim even amateur status in any of these disciplines, there have to be gaps in our treatment of the subject. Hence the work must be viewed as a contribution by geneticists to a topic of broader significance than genetics or animal breeding can alone encompass. It is presented in the belief that similar approaches by social scientists will contribute to a fuller analysis and so to better prediction of the consequences of different policies and perhaps to identifying the best courses to follow, should "best" prove to be capable of an acceptable definition. Just as the advances in human biology create social and moral problems exceeding the competence of specialists in biology, so do the advances in the production of livestock pose problems in politics, economics and sociology that cannot be solved by research workers acting independently.

It is, therefore, open to doubt whether population genetics as currently taught is as effective for guiding the practice of animal breeding as it could be. Among modern economists there is a similar dissatisfaction with classical economics which is revealing itself as an attempt to develop a *science of political economics*. Classical genetics and classical economics both have a model form that is logical and beautiful but often takes no account of the realities of organised capitalism or socialism. Both are concerned with making predictions yet make them badly because of inadequate theory and information. Starting from the desired ends, political economics considers what policies and what instruments of policy would secure them. It is the science of a participant rather than that of an observer. In genetics a corresponding development would have the purpose and ambition to apply itself to the attainment of the goals of animal breeding. Like any other discipline, it would seek to establish a code of principles from which would flow a logically unified body of knowledge: by critical and relevant research, it would provide the theory and stimulate the practice of co-ordinating the necessary political and administrative actions with the biological facts

In surveying the opportunities and problems of livestock genetics, our aim has been to integrate, not to present new data. Controversial topics have not been avoided but treated openly so that the discussions may serve as starting points for constructive thinking. Since we have no revelations to offer, and only limited truths to go by, a trial and error process of examining issues is the only way to approach a fuller understanding. Although our familiarity with them is largely based on experience in the United Kingdom and the United States, we have often supplemented it with reports from other countries.

Only a most inadequate acknowledgment of the multitude of research workers on whom we have relied can be made. With some reluctance, a policy of referring mainly to recently published papers has been followed in order to direct readers to fuller sources of information should they want them. We would have enjoyed developing each topic as it came, savouring each report and watching the unfolding of man-controlled evolution, but it has not been possible to turn over half a library in the making of this book. Like many others before us, we have not found a concise way of communicating the necessary technicalities of genetics and animal breeding to readers unfamiliar with these fields. If, however, they are prepared to take some parts on trust, they will find that the rest will offer no difficulty. In a treatise that covers the interactions of the science and practice of animal production, there are bound to be errors of fact and of judgment, but we hope they will not be so serious as to vitiate our purpose. In brief, it is to examine some of the problems raised by the recent developments in science in the light of our belief that animal breeding has a significant role to play in the welfare of mankind. The primary question to be explored is how this role could be most adequately fulfilled in the best interests of society as a whole. Animal breeding does not exist for the sake of supporting breeders, geneticist breed societies, recording or supervising organisations, but all of them serve society through animal breeding.

We wish to express our appreciation to the Agricultural Research Council for travel grants and contributions towards subsistence, and to the staff of the Natural History Museum, London, for their hospitality during preliminary work on the manuscript.

January 1966

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H. P. Donald

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CHAPTER 1

ANIMAL BREEDING IN ITS SOCIAL CONTEXT

Forecasts of the rate of expansion of the human population of the world are generally familiar. Stimulating and thorough discussions of population pressure and food supply may be found in many sources. In particular, the report of the Stanford Research Institute (1959), the symposium of the Royal Statistical Society (1963) and the volume edited by Mudd (1964) on which much of the material in this chapter is based, may be recommended.

TABLE 1.1

Past and future estimates of world population (from Stanford Research Institute, 1959, and Mudd, 1964)

Year	Population in millions
1000	275
1100	306
1200	348
1300	384
1400	373
1500	446
1600	486
1650	545
1750	694
1800	906
1850	1171
1900	1550
1925	1907
1950	2497
1975	3828
2000	6267

Table 1.1 provides dramatic evidence of the acceleration of population growth rate in this century. Even if drastic measures to control the pressure of the expected numbers were soon adopted, it is too late to achieve much reduction in the projected figure for the year 2000. Urban alienation of land now used for food growing makes matters worse, and it is difficult to escape the conclusion of Slater (1963), that by the end of our century "the farmers of the world will be faced with producing on three-quarters of an acre of cultivated land and on one acre of permanent grassland what they now produce on an acre of cultivated land and two acres of permanent grassland." No one can foresee now whether an increase of one-third of the current production on cultivated acreage and a doubling of that on grassland will be attained in thirty-five years, or whether other developments, such as the production of acceptable synthetic foods, will reduce the menace of starvation. Meantime, finding ways and means of increasing the world's food supply, and even more important, the efficiency of food production, presents one of the most challenging problems mankind has yet faced. It is, perhaps, unseemly for those who are well-fed to object that appetites grow by what they feed on, and that there is, therefore, no hope of catching up on the shortage of food. Although there may be room for argument concerning the definition of a shortage, there will surely be a greater shortage than there is now unless food production is raised to match the increasing number of mouths. Some authorities fear a losing battle against want but dissenting voices should also be noted. Thus, Clark (in Wolstenholme, 1963) estimates that 45,000 million people could be readily supported on earth, and, if survival only at the minimum caloric level is desired, ten times as many. Similarly, Mayer (1964) thinks that arable farming could be so extended and fertilisers so much more liberally applied that the problem might turn into the disposal of surpluses. It is assumed that technological advances such as *chemical synthesis of food, taking salt out of sea water, and heating* lakes by atomic energy to encourage cloud formation will ensure food for everyone. Furthermore, since space research must include the nutrition of astronauts there is the possibility of a scientific fall-out to benefit man on earth. But even if these minority views are accepted, the problem of significantly and speedily augmenting current food supplies remains. The times demand a strategy for the war against want on the agricultural front.

I. World Food Needs

It has been estimated that about two-thirds of the present population in the world suffer from malnutrition. To correct this deficiency and to

provide adequate food for the expected increase in numbers of people calls for a steady annual increase of 2·25% in the total food production in the world. In recent years the average increase has been estimated at not more than 1%. Although some areas have exceeded this rate (North America produces about 120% of its caloric requirement), others, such as parts of Asia (with the Far East producing less than 90% of its needs) actually show a decrease in food production per head when 1957–58 is compared with 1937–38.

TABLE 1.2

World protein consumption

Region	Total protein consumption g/caput per day	% of protein of animal origin	% of total diet of animal origin (milk, meat, eggs, fish)
Far East	56	14	5
Near East	76	18	9
Africa	61	18	11
Latin America	67	37	17
Europe	88	41	21
North America	93	71	40
Oceania	94	68	?
World	68	29	?

The problem is acute in respect of protein, and particularly animal protein. As Table 1.2 shows, regions of the world vary considerably in the proportion of protein in the total diet and of protein supplied by animals. North America enjoys a proportion of animal protein in the average diet eight times higher than that of a Far Eastern diet, while Europeans exist on half the North American amounts.

If the quantities of animal products in food are too small, protein malnutrition results. It has been shown that the mortality rates of children tend to rise when their protein consumption, as estimated in the last column of Table 1.2 goes down. There are, of course, many reasons other than protein deficiency for high infant mortality. Deaths from this cause for children between 1 and 4 years of age, occur more frequently than do earlier deaths partly because of the transition from breast feeding to adult diets. It is, therefore, perturbing to find that the

ratio of death rates in South India to those of England and Wales is six for the age group of 0–1 years, but rises to over 25 for the age group of 1–4 years

That the problem of food shortage is not only one of distribution but also of production is clearly demonstrated by Table 1 3 The so called food surpluses in Europe, North America and Australasia shrink into insignificance when viewed in the context of the world deficits of food

TABLE 1 3

Estimated world food deficit (from Aylward in Ovington, 1963)

Type of food	Deficit in millions of metric tons	Deficit as % of U S agricultural production
Animal protein as non fat milk solids	1 8	35
Pulse protein as dry beans and peas	0 4	40
Other protein as wheat	35 6	} 120
Remaining calorie deficit as wheat	8 6	

II Shortening the Food Chain

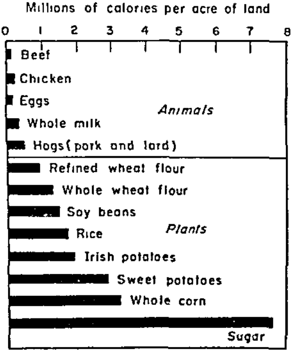
There are many means, some obvious and some obscure, by which the amount and the efficiency of food production could be increased More than a quarter of a century ago Kunkel (1938), among others, pointed out the extreme inefficiency of producing food through a lengthy chain, that is, the series of steps in the transformation of materials by living organisms which are necessary to convert energy and nutrients into edible forms If the 1 million calories per year that a man requires could be obtained directly from mineral and synthetic sources, there would be no food chain Should humans need in addition a source of protein which they could get directly from plants, there would be one or more links to the chain Animals interpose links which considerably lengthen the food chain in many instances Kunkel, who conservatively assumes that efficiency of conversion at each link is about 20% (and 10% may be a closer figure for animals), calculates that an Eskimo must consume 5 lb of seal to gain a pound in weight, each pound of seal being derived from 5 lb of fish each pound of fish from 5 lb of shrimp or other inverte brates, each of which in turn is produced by 5 lb of algae In short, it

takes 625 lb of algae to make one pound of Eskimo, with a loss of at least 99·84% of the originally available energy.

It seems that one of the readiest ways of increasing efficiency of food production is to shorten the food chain by placing greater reliance on plant products supplemented by synthetic additives to correct for deficiencies of amino acids and other nutritional essentials.

Indeed, the prospects of increasing food supplies from plants are in many ways brighter than those from domesticated animals. For instance, the efficiency in terms of man-hours required to produce a given amount of beef has increased by 13% between 1948 and 1960 (Byerly, 1962). Milk has done better with an increase of 42% and poultry better still, with 117%. Both, however, are inferior to feed grains which have shown an increase of 168% attained through improvements in varieties, crop husbandry and agricultural machinery.

Plants yield more calories per acre than do animals. Figure 1.1 from Mangelsdorf (1961) shows this in a striking fashion. Plant products are more easily transported, require less labour and are consequently cheaper. Against these formidable advantages, however, can be placed a tendency to be bulky, less digestible, and deficient in certain amino



According to some writers, the increasing world demand for food will lead to such an expansion and perfecting of industrial methods of protein production, that they will quantitatively overshadow traditional farming. Whilst it might be rash to deny this possibility, there seems to be no reason for expecting any sudden responsiveness to existing needs that would make animal production superfluous. As yet margarine has not displaced butter, nor synthetic fibres, wool. Such has been the recent increase in production on each acre of land in Europe and North America that the power of livestock to compete with chemical industry may in fact have the effect of postponing the development of substitute methods. This would be regrettable if it meant less progress towards enough protein for all.

While, therefore, on a pessimistic view, the future may lie with the vegetarians, there is good reason now for the omnivorous to fight a strenuous rear-guard action by improving the production of animal protein from fish and livestock. Furthermore, the maximum output of protein and calories may be achieved by mixing animal and crop husbandry. To some extent this follows from the advantages of using grass in rotations, and to some extent from the use by animals of surpluses or of by-products such as wheat bran, sugar-beet tops, fish meal, and poultry offal, as well as from manuring of the ground. Livestock are likely to remain important especially in areas unsuitable for cropping, at least until research has devised ways of making them suitable. Meantime research helps livestock production in these areas through discoveries about grazing management, plant species, and nutrition. Urea, for instance, has been found valuable as a substitute for part of the protein needs of grazing animals where protein supplements would be expensive. Research may show how to adapt rumen flora to cope with larger quantities of urea and raise further the nutritive value of rough pastures.

There are social aspects to land use which may require the maintenance of traditional methods, inefficient as they may eventually become in comparison with chemical processes of food production. Soil fertility must be conserved to ensure an acceptable environment for man and he may find it a long and painful process to adjust himself to the vicarious new world of synthetics. It may appear imperative to the next generation, if not to this one, to protect the countryside from pollution and the by-products of industry, from depopulation, from erosion and misuse (Udall, 1963). Ecological stability in some areas may be best achieved by farming methods involving grazing animals, and this stability may have to be maintained by a tax on urban activities. Involved in this is the widespread social problem posed by the declining status and income

of the small farmer unable to raise the output and efficiency of his farming (Hoogschagen, 1958; Organisation for Economic Cooperation and Development, 1964).

The post-war expansion in science and technology is raising the general standard of living in which those who reside in the country wish to share. Rural industry, like urban industry, is moving towards the use of more capital, less labour, and higher outputs. Within the context of small family farms, these changes are difficult to accomplish but there are a number of adjustments facilitating them (Ahlgren, 1962). Farmers may increase the size of their farms or, alternatively, seek part-time work elsewhere. They may embark on contract farming so that risk capital can be provided by larger enterprises. They may place increased reliance on purchasing and marketing co-operatives. By some means augmented productivity and higher real income must be achieved for the diminishing country populations. This is not primarily a genetic problem but there is a genetic element in it. Even if the bulk of research effort is devoted to the development of industrial food production or of stock especially adapted to intensive enterprises, traditional kinds of livestock on the farm could also be subjected to improvement as a matter of national agricultural policy.

III. Genetics and Breeding

In the course of a long history, animal breeding has experienced many changes in its theories and its practices. But until recently it has never been obliged to adapt itself precipitately to new conditions. All at once, however, events seem to conspire to destroy the old order. Genetics is becoming indispensable in livestock breeding. Economic pressures to intensify agricultural production, rising standards of living in the country as well as in the towns, and technical aids such as artificial insemination, computers and reproduction of data have combined with the maturing of the science of heredity to put the system of pedigree breeding under severe strain. This system has been an integral and essential part of the industry that produces milk and meat. Consequently, everyone in a world already short of animal protein has an interest in its future. At this juncture in the affairs of countries where some version of the pedigree system has been used, it might then be useful to consider how well it fits in with the needs of modern animal production, and whether changes are desirable from the standpoint of general welfare.

As farming enterprises grow larger, their managements have to equip themselves with information and resort to technologists to help them

reach decisions and plan for more distant goals. Industrial developments of this kind widen the range of farming activities, since the old style farmer, sensitive to local markets and operating on hunches, remains as a contrast to those for whom farming is rapidly becoming more of a programme than a way of life. There is now manifest a spectrum of personal attitudes varying from frankly revolutionary to backward-looking. Many livestock breeders still do not know Mendel's laws announced 100 years ago, so that in the struggle to feed the world's growing population one of the main industries producing protein is found to be largely based in practice on breeding methods that owe little to modern genetics.

In Western countries the completely remodelled poultry industry exists along with a sheep industry notably reluctant to modernise itself. In many of them, including some with advanced industrial technologies, the administrative machinery of governments and agricultural organisations relative to animal breeding appears to be roughly coeval with sheep breeding methods. Yet all parts of all industries must thrust and strive, or lapse into stagnation. To adapt the outmoded ways of thinking that are enshrined in official attitudes and policies is therefore often as urgent a task as to improve the efficiency of livestock. Agriculture has long been regarded as conservative in its outlook and indeed in the less intensively farmed areas the adjective is probably justified. However, in the more intensively farmed areas, there have been many developments which stand comparison with those in the most progressive of other industries.

Statistics and genetics have no more destroyed animal breeding than chemistry has destroyed biology (Commoner, 1961). They are powerful allies and should be treated as allies by animal breeders. If geneticists advise that a trait has negligible heritability, then it is a waste of time selecting for or against it until some way is found of increasing the available genetic variation. If statistics show that twenty offspring are needed for a meaningful progeny test, then it is no good pretending that two or three are enough. Without aims, however, genetics and statistics are futilities for they cannot generate them. They are incomplete in themselves and are not an industry.

A reasonable scepticism regarding the assertions of scientists is proper. The operative word however is "reasonable". Scepticism is often a cloak for ignorance and as such is unprofitable. A well-informed scepticism that reveals and advertises weaknesses in theory or in factual support can provoke further research that justifies or demolishes it. It is too valuable a weapon to lose by getting it confused with obscurantism, ignorance or unwillingness to face facts.

Among scientists there are individuals of varied abilities, and diverse training. Not only are they far from equal in skill at expressing themselves but they differ in degree of self-criticism and in native intelligence. There is no need to assume that they are individually or collectively always right or always wrong. But it is operationally wise to recognise when they are expressing well established and generally held scientific beliefs which are as close as one can get to real if limited truths.

A geneticist can be as much a prisoner of his theories as a breeder. To shrug off conflict between the biologist and the practising farmer by saying that there is something to be said for both sides is not enough. Not one but many conflicts occur and their best resolutions are not always compromises. Breeders are shackled by tradition, by doubts about genetics, by financial worries, and by personal objectives. On their side, geneticists may err by oversimplifying, by relying on inadequate data, by their personal scientific ambitions, and by the fact that many of them carry no burden of financial or administrative responsibility. For the creative scientist, as for the creative breeder, reason is the handmaiden not the master. Both are artists and they should understand each other well. Every man in fact is in part an artist shaping his own life, moving and touching other lives. Since human affairs cannot always be intelligible unless seen as a whole, it would probably be better if genetic theories were more fully tested and exposed by a well-informed opposition. With such a paradoxical impossibility, it is incumbent upon geneticists to keep the edge of self-criticism sharp. As Price (1964) points out, there can be no acceptable non-scientific critics of science. The mystique of science is such that opinions about it are sought automatically from eminent scientists. The generals of science must find from their own ranks the strategists, administrators, historians and economists although their qualifications for making *ex cathedra* statements in these capacities are dubious. Their public image notwithstanding, scientists are not cold and objective men in white coats proceeding with infallible scientific method and impersonal conclusions. With so much ambient mythology, there is a risk that when misplaced enthusiasms or erroneous claims made by individual scientists are discovered, they will be attributed to science itself.

An example from the past is easy to find. Not only did many of the early Mendelians, in the excitement of the dawn of the new era in the study of heredity, insist on having the key to animal improvement, but it also took the next generation of geneticists, now working on the population level, some time to arrive at reasonably sober estimates of the power of their genetic tools (compare, for instance, Lerner, 1950, with Lerner, 1958). The occasional yielding to the temptation that

scientists felt to meet adverse propaganda with half truths and scepticism with unjustifiable assurance has undermined the research worker's special claim to be heard Animal breeding is not the exclusive preserve of either pedigree breeders or of scientists It is appropriate to recall in this context Oppenheimer's (1963) gentle advocacy of a proper humility in scientists ' it would perhaps be good if in talking (to our friends in other walks of life) we could count on a greater recognition of the quality of our certitudes where we are dealing with scientific knowledge that really exists, and the corresponding quality of hesitancy and doubt when we are assessing the probable course of events, the way in which men will choose and act "

IV Social Implications

The word revolution is not too strong for the consequences of artificial insemination in dairy cattle breeding or of big scale operations in the poultry industry (including the technologist's mode of thinking about breeding), but it is hardly applicable to large animal production In spite of all the spectacular advances over the whole range of agricultural problems, world productivity rises relatively slowly To integrate and exploit an advance even a simple one within the enormous complexity of agriculture takes time It could happen and probably does happen that technical progress on occasion outpaces human adaptability in some directions but to damp down research and development on this score may well lead to difficulties in re animating it when the need arises

The results of applying science to the breeding industry cannot be properly assessed in isolation from the other elements, such as education, the availability of computers the changing character of consumption and the economic policies of governments One instance is the expansion of scientific endeavour which has coincided with an increase in the size of individual breeding establishments in the post-war years Not only do these phenomena represent a trend characteristic of the times but more important they interact with each other

The growth of scientific *information* places a premium on the operational size of a breeding enterprise since only the bigger establishments can obtain and apply much of it Reciprocally, the larger and the more integrated an economic unit dealing with animal improvement is, the more it can contribute to the pool of new knowledge

Interaction of this sort is a universal phenomenon Modern biologists (exemplified by Dobzhansky, 1962) look upon human evolution as a continuing process involving much more than either biology or a history

of cultures. A mutual feedback between biological and social factors is what moulds the history of the human species. With reference to domestic animals, this is a particularly fitting concept, since they have always been regarded by man in an anthropomorphic way, as if sharing his attitudes and feelings. Class distinctions, the prohibited degrees of relationship between mates, emigrations and immigrations occur both in man and the animals under his control with varying frequency or intensity depending on what has gone on before. The future of animal breeding, therefore, will not be the outcome of theorizing nor the result of wishful thinking but a response produced by the interaction of biological realities of livestock production with changing human culture. Neither the exact challenge nor the actual responses are predictable, but there is certainly no dearth of possibilities.

In general, the social implications of science have attracted increasing attention since Bernal (1939) as a natural scientist emphasised them a quarter of a century ago (see Goldsmith and Mackay, 1964). Although much has happened to bring nearer his vision of a "socialized integrated scientific world organisation", there are obviously many economists as well as humanists who deplore such a future. But whatever view may be taken of socialism on the one hand, or the gaps between the two (or more) cultures on the other, there is agreement that the scientific method should be used to limit and preferably eliminate such a palpable evil as starvation, and to improve man's lot on earth. Bernal himself considered that no culture could stand apart from the dominating practical ideas of an age without becoming pedantic and futile. He was not considering any specific patterns of behaviour, let alone that which governs activities in the field of animal breeding, but what he says of the whole applies equally forcefully to the part.

Culture has been viewed by Bose (1961) as an adaptation aiding the survival of communities which is based on a constellation of ideas and emotions. When new adaptations are required in the name of biological fitness, cultures must change and become more complex although not in any predetermined way. Over the centuries there has been a sequence of ideas and emotions on the subject, each giving way in its turn to another more in harmony with its time. Perhaps it has always been the fate of animal breeding to suffer some degree of disharmony with the trend of events. Geared as they are to the slow rhythm of the seasons and compelled to endure long gestations, domestic livestock engender a certain tempo of thought and action in those who breed them. This is unfortunate in Europe and North America but doubly so in Africa and Asia. Old ideas and institutions tend to outlive their usefulness and become over-valued. They lose initiative but continue to be supported

out of habit or pride. Yet there is an urgent need to adapt them to changed conditions and at times to have the courage to abandon some of them completely. There is no aspect of animal breeding that research has left untouched; there is no breed that is perfect; and there is no system of breeding that could not be improved. Adaptations, of course, will come sooner or later, but sooner and more smoothly if consciously sought by flexible minds.

V. Decision Making

One of the most pressing and yet neglected problems in animal breeding concerns decision making. It is easy to look back and see how technical achievements lead to the concentration of power in few hands. What has happened in other industries is also happening in agriculture. The growth of large businesses based on vertical or horizontal integration, the breeding of a million cattle by a single artificial breeding organisation, and the control of prices by government action, are three well-known examples that leave no small-scale breeder untouched. In each case, a few people make decisions affecting many. This is a social problem with considerable effects on animal breeding because of its susceptibility to being organised. Breeding has been so vague in its objectives, so inefficient in its methods, and so rudimentary in organisation that it offers great scope for the modern decision-maker. In many situations this may turn out to be the scientist, unconscious perhaps of his influence, but a decision-maker none the less. Churchman (1961), whose studies of this subject make enthralling reading, goes so far as to say that science *is* decision-making. In his sense, the sense that scientists determine what information they will collect and how they will interpret it, this conclusion is inescapable. Scientists, however, are not the only decision-makers in the new forms of animal breeding although they obviously influence the nature and the quantity of data provided for those who do make decisions.

Those who are at home on the frontiers of knowledge can become very powerful, but they are few and often do not communicate easily with other people. There are sometimes problems of communication between management and technologists; how much wider, therefore, is the gulf between the latter and the ordinary farmer. Important though it is to those concerned, this question is but one facet of the vastly greater one of informing the voter in a democracy about the political issues involving science

The organisation of animal breeding has heretofore been a haphazard matter. Neither the responsibilities nor the prerogatives of scientists

and managers, breeders and bankers, private concerns and the state, are sufficiently clearly defined anywhere in the world to allow a simple analysis of the genetic consequences of the various developments taking place. Yet the combination of big science and big business results in the emergence of a whole set of new problems of vital import to the future of mankind under any form of government. The genetic management of our resources of useful or potentially useful animals is one of such problems, and discussion of it is the main purpose of the present work.

CHAPTER 2

THE WAR ON HUNGER

The purpose of this chapter is to describe briefly the agricultural background against which the potentialities of animal breeding are to be considered. Into the intricate fabric of agriculture are woven many minor patterns which, being all functional parts of a whole, cannot be comprehended separately. If animal breeding is to meet the calls on it, those who are responsible must ensure that its objectives are generally acceptable to society and that its methods are consonant with its purpose. There can be no hope of bringing in a few painless adjustments intended to stave off radical changes. As a reminder of the exciting developments in many agricultural practices which will influence and be influenced by types of livestock, a few pages have been culled from the works of recent historians, research workers and commentators. Inadequate though they are to give more than hints of the ferment of ideas, they may serve to show the need for a continuing adaptation of all the sciences and practices to each other. Only a little imagination is required to foresee changes when a strong demand, a flourishing technology and a relatively underdeveloped industry are in conjunction.

ing the use of enclosures, the provision of winter feed and pastures of clover and artificial grasses. Later, the activities of Robert Bakewell and his immediate successors laid the foundations for the structure of animal breeding as it is known today. These breeders owed their opportunity to the increased demand of city markets and to improvements in road, rail and water transport both within the country and for export of live animals from Britain. The techniques of breeding thus established then began spreading to other countries. In many instances, livestock production depended on locally developed methods, but, by and large, where it became organised, its structure was based mainly on the British model.

TABLE 2.1

Trends in yields of crops, milk and eggs in the United Kingdom

Item	Pre-war average	3-year average *1960–63*	% *increase*
Wheat	17·8 cwt/acre	31·3	76
Sugar beet	8·2 *tons/acre*	*13·0*	*63*
Potatoes	6·7 tons/acre	8·9	33
Milk	560 gall/cow	777	39
Eggs	149 eggs/hen	191	28

The nineteenth century brought a steady increase in productivity through the spread of improved husbandry. At the same time considerable changes were effected in the conformation of animals before as well as after the compiling of herdbooks began. How much genetic change in milk yield has taken place is problematical, but greater fleece weights (in Merinos and Romneys), smaller fleece weights (in Wiltshire Horns), more eggs (in ducks and hens), and faster growth (in pigs) have certainly been achieved in the comparatively recent past. All these adaptations took place in the context of developing markets and changing husbandry. In his book Ernle (1961) has traced the main lines of development in agriculture in the United Kingdom which in many ways are also typical of other countries. The one word which comprehends all the changes, regardless of time or continent is intensification. During the eventful period 1910–50, the tempo of change quickened. Under the impact of scientific discoveries coming ever faster and being applied promptly, the old rigidity of both plant and animal production, expressed in fixed rotations and other rules of good husbandry, had to give

way to a new adaptability all over the world (Russell, 1954). Advances are still coming rapidly. In the year ending May 1964, net output in Britain was nearly a quarter more than it was ten years earlier. In this same period, the number of agricultural workers fell by over a quarter due to the mechanising of traditional farm processes and the saving of labour by modern methods. As with output per man, production from both crops and animals is rising, but more slowly for the latter. Table 2.1 shows how the output of several products has grown in the United Kingdom since 1939, and similar figures are available for other countries.

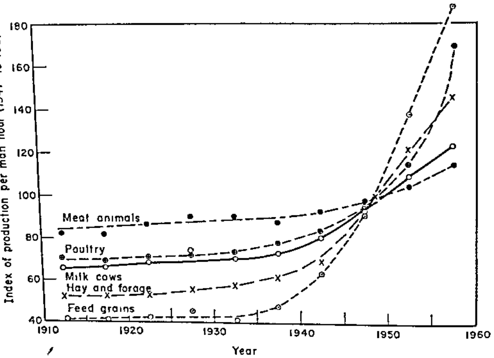


Fig 2 1. Man hour output in livestock and crop production (from Byerly, 1964; reproduced with permission of the author and publisher)

For instance, a very similar process has been going on in the United States Figure 2.1 (from Byerly, 1964) shows how the output of five major products per man-hour took a marked upward trend between 1940 and 1959 Between 1925 and 1940, the annual number of eggs per laying hen rose from 112 to 134, an increase of 1·5 eggs per year. By 1960 the number of eggs rose to 209, the rate of increase having speeded up to 3 75 eggs per year.

Again, in the countries with advanced dairy industries there has been a general upward trend in yield of milk (or total fat) and in herd size, since 1945 (Table 2 2). Since this trend is so fast, so widespread, and independent of breed, it seems likely that much of the increase is

attributable to higher levels of husbandry, such as more liberal corn feeding of cows in the United States.

Although net financial outcome of farming operations is the major factor governing them, it is not the only one. Livestock farmers have often a loyalty or personal attachment to their stock which makes them

TABLE 2.2

Trends in dairy cow production

Country	Breed	Period (years)	Increase per year kg butterfat	Increase per year gall milk
Denmark	Red Dane	15	2·7	14·8†
	Jersey	15	2·7	14·8†
New Zealand	Jersey	16	1·3	7·2†
Holland	Friesian	12		5·3
England	Friesian	15		10 0
	Ayrshire	10		9·2
Scotland	Friesian	7		7·4
	Ayrshire	7		8·1
U.S.A.	Holstein	4		16·2
	Ayrshire	4		18·5

Comparisons between countries are not recommended owing to the varying methods of estimating average yields and to the unequal periods for which data are available.

† Based on 4% butterfat equivalent.

reluctant to abandon either their profession or their animals contrary to what economic pressures tell them to do. Others hope vaguely (and, usually, vainly) that things will improve if they can hold on long enough. There has been, consequently, a time lag in the multiplication of economically superior animals and in the demise of inferior ones. As farming becomes more of a business, this time lag is likely to become shorter. With the growth of performance testing and the intelligent analysis of the results, the merits and demerits of particular breeds and crosses of sheep and cattle could become widely and quickly known as has happened with pigs and poultry. It may be some time yet before new varieties of the larger livestock are bred to meet specific conditions of production as poultry are now, but they are in clear prospect.

Poultry are now bred largely by careful combinations of lines to have a uniform rate of growth and mature body size, to produce a large

number of eggs of specified size and colour, to have high food efficiency, and to present an attractive carcass. All these characteristics have been notably improved while the cost of eggs and of poultry meat has been reduced in the last two decades. The eye judgment of breeders played no part in this process. In the task of improvement of such traits as disease resistance, appetite, ability to utilise various diets (for instance, soya bean meal which is deficient in methionine), laboratory techniques applied purposefully on an adequate scale are necessary.

Many of those who produce other types of stock still have to learn the lessons from poultry: costs of production at all stages must be decreased as far as possible; market requirements met accurately; growth rate and production increased; food efficiency improved; the number of separate products or qualities reduced to a minimum; husbandry mechanised; fertility raised and mortality lowered; overheads spread over a large production and all unprofitable activities eliminated.

Since many livestock farmers do not yet see the need for records of performance of their stock and thus have only a vague idea of the strong and weak points of their businesses, it might appear that they, in general, have a long way to go before they can take advantage of recent technical developments. This was true also of the numerous small poultry farmers who no longer exist as independent producers. What happened in their case was that they first provided a market for improved varieties and then were forced by economic pressures to quit the industry or become absorbed by more efficient enterprises.

Books on medieval agriculture show that stockmen flourished long before specialist breeders. They had the task of drawing a usable surplus from their animals under very primitive conditions, and in skill and devotion to their charges concede nothing to their successors. With the advent of shows and then pedigree breeding further opportunities were created for them to develop their expertise and authority to the point where they reigned practically supreme in their departments of the farms. They could no doubt extract the best out of their herds and flocks by a fine sensitivity to the needs of individual animals in a farming world which could be lavish with cheap labour. It is to be feared that, like many other kinds of craftsmen, these artists are losing status in industrial farming. Where dairymen are judged by the number of cows milked in an hour, there is no place for the slow milking cow or the man who will patiently milk her out. There is no place for the time-consuming hurdle flock of sheep, for the small flock of chickens maintained under extensive conditions, or for the sow that must be watched while she farrows. By degrees all classes of stock are being subjected to

selection which favours animals that need a minimum of individual attention. The contrast between the heterogeneity of colour and form of pre-purebred *flocks and herds, which made visual identification* of individual animals easy, with the monotonously uniform appearance of strain crosses of chickens is a reflection of this process

Just as new varieties of crop plants have to be suitable for the new machines to sow and harvest them, and, more recently, for the animals that will eat them, so the test of a better animal must be conducted under advanced conditions of livestock production. There seems little doubt that stockmen and breeders will also have to prove themselves under the same conditions

The basic difficulties about raising livestock production in either developed or under-developed countries are sociological rather than economic or scientific. They include religion, systems of land tenure, and a failure by "economic man" to live up to his name. The extent to which farmers are unresponsive to the profit motive would make an interesting study. Whatever the reasons, however, many are strongly resistant to infringements of their chosen occupation. When the result of this is a failure to increase or cheapen production, the world is the poorer and, where there is no surplus, so is the taxpayer or consumer.

II. Recent Advances

A. Husbandry

Much of the increased productivity of the land has come from drainage, provision of winter feed for stock, improved cultivations, especially from the speed and power of tractors, fencing and fertilisers. Although these techniques are hardly recent in conception, they are still being refined and are capable of increased utilisation (Cuthbertson, 1963). In particular, the use of fertilisers can be extended as higher yielding crop plants and grasses become available and as heavier stocking rates compatible with good health become possible.

While seeing some scope for reclamation of both high-lying and low-lying ground, Russell (1954) thinks that the greatest potential for increasing production lies in more effective use of the land already occupied. No doubt this would require the transformation of nomadic and subsistence farming with all the social consequences of such change. In order to place farming on the spiral of increasing productivity, systems of land tenure and of providing capital would have to be adjusted to permit the full exploitation of the soil. Russell supposes that this transformation has already taken place in Northwest Europe and North America but the process has only begun.

Advances in the sciences of plant breeding and animal nutrition and animal health are of the greatest significance to animal breeders. In fact, for a well-balanced assessment of future prospects in animal production they can hardly be considered separately. As might be expected, this is most evident where growth is fastest (whether it be growth of animals or growth in human skill) and this is at the most intensive end of the scale of agricultural activities. Pig and poultry producers have accordingly appreciated, as have dairy farmers, the newer knowledge of nutrition that permits them to use well-balanced rations that are based on the mineral, amino-acid, and vitamin needs of high-producing stock. Sheep and cattle farmers are gradually taking advantage of the better yielding and more palatable strains of crops, including grass. All kinds of stockmen become increasingly dependent on the ability of the veterinarians to steer them clear of disease.

Machinery for automatic feeding, watering, ventilation and cleaning of animals is already in common use for poultry and for beef cattle in feedlots. There seems to be no insuperable obstacle in the way of extending such methods to other classes of livestock which repay intensive rearing. Another well-known development is the use of antibiotics and other drugs for augmenting production and for hygiene. Just what the future holds in this respect is not obvious, but it is certain that as new methods of husbandry arise there will be a need for coping with diseases that may not have been important formerly but have become important under new intensive conditions Minimum-disease and specific-pathogen-free pigs have an obvious bearing on this problem. This potential seems to be high. Disease takes a heavy toll of intensively kept animals and it seems likely that future housing will be associated with means of obtaining and maintaining animals which are free of certain diseases. Among the features of these buildings will be automatic feeding and temperature control. The latter is important because it affects efficiency of food utilisation and, through it, rate of maturing. Temperature control may also be of significance in the kinds and levels of incidence of disease which stock experience.

B. Artificial Insemination

Since 1945 artificial insemination (A.I.) of dairy cattle has provided new and great opportunity for advances in livestock production. It soon justified itself on economic grounds. But contrary to original expectation, finding suitable sires for artificial insemination centres proved very difficult. As a result, the recording of performance had to become highly organised. In the long run, the repercussions of artificial insemination of

dairy cattle on other kinds of livestock, through the complementary development of operational research, deep freezing of semen, and progeny and performance testing, and the attitudes of farmers to them, may be more important than artificial insemination itself.

Naturally enough, the main benefit of using this technique accrues to those who control the intellectual and physical machinery of its operation and to their employers. Some breeders of pedigree dairy cattle, however, suffer a loss of trade for young bulls, and also a loss of prestige, since their breeding methods seem to be inadequate when put to the test of performance. With the spread of testing to pigs and sheep, there will be the same disagreeable revelations about the way these species are being bred. The effects of A.I. in cattle are more fully discussed in Chapter 6.

C. Genetic theory

During the last thirty years, the theory of population genetics has become a solid basis for industrial planning. Generations of students have been taught its precepts and speak its language. As a result of their activities, a large store of genetic information about livestock has been collected and made available to all. Statistical methods have been devised for use in the specific problems of animal breeding and widely applied in many countries. With the coming of machinery for the handling of data, culminating in the computer, the geneticist became possessed of very powerful tools for manipulating livestock populations. Examples of his use of these tools to good effect is to be seen in the dairy, pig and poultry industries. In addition, publicity in technical and popular journals for scientifically gathered and interpreted data has created a new social atmosphere in which breeders must now work. The mystique of stock sense has become an uncertain refuge, as has the green thumb in mechanised plantations.

A comprehensive theory has been provided for understanding the biological evolution of livestock. As it becomes more refined, its strength will increase, but it is already too firmly established to be wrecked or even shaken by personal distaste for its conclusions. Although there may well be on occasion some sentimental or political objections to their logical consequences (for instance, financial embarrassment to pedigree breeders), these conclusions will not on that account be less valid. Chapter 3 is devoted to a fuller discussion of modern genetic theory.

D. Marketing

Off the farm, marketing has been growing in complexity with the aid of cold storage, grading, rapid transport and packaging. Farmers and

the breeders who supply them with breeding animals must reckon with the results of consumer research and advertising. They must expect that elimination of hard physical labour, propaganda of a medical character, super-marketing, deep freezing and freeze-drying, and a growing interest in quality and hygiene will have repercussions on farms such as the practice of contracting for specific products. For evidence of this they need only recall the increasing preference for meat that is free of fat and is tender. Consumers have also obliged sheep farmers to share their wool markets with manufacturers of artificial fibres. Furthermore, rapid traffic in both live animals and carcass meat which is now possible between countries makes a producer sensitive to changes in supplies occurring far from his own parish. Yet it also provides opportunities of selling in wider markets such as were taken by the United States broiler and the Danish bacon producers. Political and economic considerations may determine whether markets are protected and prices buffered, but biological facts are also determinants of uniformity of products, efficiency of production, and the long-term outlook for the development of superior strains.

These are, perhaps, the principal changes of immediate interest to animal breeders but they will be followed by others in the near future. Evolution is not mere change. It is the replacement of simpler systems by more intricate and more complex ones. There is no prospect, therefore, that any reversion to former and less exacting concepts will occur.

It is as much a law of livestock breeding as it is of natural evolution and of the history of human institutions that the most rapid development occurs when new ecological or social opportunities arise. In livestock breeding, the opportunities are greater than ever, since the authority of formalism in breeding has been broken at the moment when scope for exercising the new liberty is expanding. Animals must now be bred not for their fair appearance but to fit the machinery of mass production.

III. What Is Improvement?

Possibly one of the greatest difficulties facing breeders, agricultural organisations, and geneticists is how to reach agreement on what changes in performance constitute improvement. This is hardly surprising. Three elements, each complex, are involved:

1. pedigree breeders' incomes, unlike those of users of unregistered stock, include the sale of pedigree breeding stock;
2. performance has many components, some of which may be incompatible with each other;

3. economic and environmental conditions of production are inconstant, *prices and husbandry varying with time and locality.*

Pedigree breeders have a readily understandable point of view. As long as breeding stock is bought on appearance, they are there to supply the market. They must foster the popular type by whatever breeding, husbandry or advertising methods they have at hand. They are fully entitled to give it as their opinion that a certain balance of characteristics, that is, type, is desirable and that they are providing it. Others are equally entitled to different opinions.

The owners of commercial cattle or pigs or sheep are aware that their net income is affected by many items in a profit and loss account other than milk yield per cow, the number of pigs in a litter, or the weight of a weaned lamb. They have not, however, been very well informed by research workers about the importance of other components of net profits, such as outputs per man and per acre, mortality and veterinary expenses, the salvage value of worn-out breeding females, and their rate of depreciation. Although familiar, these items are rarely studied by geneticists. There is consequently not much information about the amount of genetic variation in them; nor is there likely to be much until suitable data are collected. On the assumption that they are of low heritability and unlikely to deteriorate as an unfortunate side effect of selection for weight of meat or milk, it is thought by some to be reasonable to ignore them in breeding.

Many advocates of positive eugenics, who have a vision of breeding a superior race of men, find it hard to persuade others where superiority and breeding value lie. Improvers of livestock face the same difficulty. Since there is room for disagreement, the pessimists can be expected to opt for attention in breeding to numerous criteria and a preference for no change. They have the advantage of being able to point out how uncertain markets are and how unreliable the estimates of costs of production. Changes in public taste can alter quality differentials in milk or meat very quickly. Technical developments in prospect could alter prices and costs substantially as, for instance, in such items as the housing of sheep, the timing of lambing, or the preparation and marketing of convenience foods instead of carcass meat.

The various authorities influencing animal breeding (poultry now excepted) have not seen fit to secure much help from those trained in the methods and approach of economics—a remarkable omission in a large industry. How does it come about that agricultural economics has not penetrated at least into research on animal breeding? Could it be that *a combination of disdain by scientists and lack of imagination in* economists has produced this result?

A negative attitude to change, no matter how well-founded, is still unpalatable to optimists and to most scientists who live by it. They can point out that over the centuries during which agriculture has reached its present stage of productivity, the trend has consistently been towards high performance and risk-taking. Occasional disastrous droughts have not prevented Australians from increasing wool production from Merinos, even at the cost of some merit in meat, milk and fertility. Claims for great hardiness have never helped a breed such as Soay sheep or Longhorn cattle that lacked potential for a saleable commodity. Unfavourable genetic correlations, making it impossible to combine all the components of perfection, no doubt exist but they may not be serious. Some of them may be counteracted by husbandry, others overcome by selection, while still others may require that some losses are put up with in order to enjoy greater gains. Although some attempts to raise livestock production by breeding may fail, those which succeed will lead to the replacing of breeds that remain static.

In the last resort, discussion about objectives in improvement resolves itself frequently into disagreements about land use. Good growth rate and food efficiency may be desirable everywhere, but the conditions under which these traits are to be manifested vary widely. Beef production, for instance, may take place in feed lots with high energy diets permitting slaughter at 1–1½ years of age, or on extensive grazings with low energy diets, periods of shortage, and a suitable weight for slaughter at 2–3 years. In southwest Scotland, for example, Galloway cattle are bred for adaptation to wet cold winters with silage feeding. To fit in with the farming system in use, the cattle must be of the right size and fatness to kill when 2–2½ years old. Too much emphasis on growth rate might disqualify them for this purpose. Since, however, there is nothing immutable in farming systems, those who control the fortunes of this breed are faced with the risk that, if husbandry intensifies further, a faster growing breed might prove more popular.

Efficiency is also wanted in straight-bred beef cattle or in various crossbreds from dual-purpose and dairy cows. Selection for growth rate, therefore, might be imposed on all breeds, but the attention paid to other things would vary in kind and intensity depending on the use to be made of land. For the British Friesian breed internal tensions are created in this way, since it is the source of much British home-produced beef. Some users require steers for a production system aimed at rapid turnover and early maturity for slaughter, others require steers for pasture and silage feeding, while still others apply intermediate methods. Type varies with rate of growth and age, as well as with beef

and dairy character. General agreement on type, therefore, for an animal that is primarily a dairy cow, but also an important beef producer, is evidently impossible. As history shows, there are several ways of escaping from this conflict of purposes: splitting the breed into sub-breeds, organised crossbreeding, and changing to another breed.

Faced with the growing world shortage of animal protein aggravated by the increasing demand for beef as standards of living rise, the administrators and sponsors of long term genetic research with livestock have a problem in deciding what resources to devote to the question of raising beef supplies from dairy cattle. As Plowman (1964) and many others have pointed out, more beef can be had from a fixed population of dairy cattle by keeping cows longer, raising all surplus male and female calves to greater live weights, using bulls of the largest breeds, and reducing losses from disease and infertility. Except for crossbreeding, these methods are all well-known and applied during the growth phase of any breed when prices are high. More beef, however, means less of something else, and beef is the most expensive form of animal protein to produce. An indirect expense that may be incurred is the loss of efficiency in improving the production of milk protein, especially if the criteria for selecting dairy cows are modified to allow for more pressure on meat qualities. This difficulty does not arise if selection for meat is carried out on a beef breed used for crossing with dairy cattle.

Similar problems of defining priorities face the breeders of sheep and pigs. Breeders, producers, manufacturers and consumers all have *different approaches to the question of what is wanted and, if agreement* by all to every change was required, it might well be impossible to reach in respect of any numerically strong breed. There is no group of people with special insight who can be relied on to have the right answer, although in retrospect it is easy to see that in the past some were nearer to it than others. During the past 200 years alone, many hundreds of local varieties must have failed and, at least, in some cases it was probably not bad luck but bad judgment that brought misfortune. Breeders of Percheron horses, Middle White pigs and Merinos could hardly be blamed for becoming redundant in the United States, in the United Kingdom, and in the hills and plains of New Zealand, where economics demanded tractors, less fat, and export lamb; but the Clydesdale horse with feathered feet, the Vermont Merino with overwrinkled skin, the rainbow type hog or the long resistance to polled varieties of cattle, were surely errors of judgment.

Such minor tragedies, nevertheless, had, and have, a major advantage. Most of them occur within breeds, but some, like those just mentioned,

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Such minor tragedies, nevertheless, had, and have, a major advantage. Most of them occur within breeds, but some, like those just mentioned,

affect whole breeds because official breed type happened to be wrongly conceived. It is the price of progress that many attempts to find it should fail. To be limited to making one attempt either because of authority at the centre of a breed association or of another type of organisation, or because numbers of animals in a breed are small, means taking a grave risk that errors of judgment will not readily be detected or corrected.

IV. Short-range Objectives

Making the best of the material and institutions now available involves a critical appraisal of animals, enterprises and industries. All three have attracted recent scrutiny from farmers, biologists of various kinds, economists, and business men. As a result, livestock production is in the process of abandoning many of its old principles and of trying to discover new ones in an intensive search for efficiency in the use of land, labour and capital.

A. Improving animals

To say that the immediate task of breeders is to improve efficiency is not very helpful, since numerous changes might be claimed to lead to higher efficiency. To select for certain traits involves risks of misreading future markets but risks must be taken by someone. Waiting for full knowledge, or striving to maintain or "improve" animals in all respects simultaneously may be the correct policy for a fraction of a breed. Should other more positive policies succeed, this fraction can then be discarded.

Until the appearance of large breeding enterprises animal breeding was a form of self-expression for many of those attracted to it, of whom some could be relied upon to be individualistic in their aims and methods. Only for short periods during the formative stages of a breed would unity of effort be achieved. This is one cause of inefficiency of the current pedigree system, for it is organised to suppress all but minor deviations from official type. Therefore, while securing the advantages of diversity is a long range problem, the present need is to encourage the breeders who will concentrate on improving performance at some cost, if need be, to type as officially defined. This kind of breeder is more likely to be found among the young and among those whose herds and flocks have currently a limited value. If they succeed in creating better adapted varieties, it is probable that type will be redefined to suit the stock they produce.

These remarks do not apply equally to all classes of livestock. In poultry breeding there has already been both a ruthless sifting of breeds and varieties for suitability to markets and husbandry, and remarkable improvements in both broilers and egg-layers. Further improvements are becoming increasingly difficult to obtain. As a result, the question of securing genetic diversity looms much larger in the poultry industry than it does with cattle, sheep or pigs, which are in a more rudimentary stage of organisation.

TABLE 2·3

Changes in rate of gain and efficiency of feed utilisation in pigs (from Ellis, 1964)

Year	Average daily gain, lb	Feed per pound gain, lb
1910	1·1	4·5
1920	1·3	4·6
1930	1·2	4·5
1940	1·4	4·1
1950	1·5	3·6
1960	1·6	3·5

for food efficiency will eventually require some constancy of the feeding system and of the conditions of production such as rearing, fattening and age or weight at slaughter. One of the points to keep in mind is that growing bacon or pork pigs are not the only members of a herd that must be fed: pigs that die of disease and accident, pigs that suffer chronic infections, pigs among the breeding stock that fail to mate or conceive promptly and completely, all waste food. Another point to remember is that an efficient pig eating only 3·2 lb of dry feed for each pound of gain in live weight consists very largely of bone, gut, skin, water and fat and only 10% of it comprises edible protein.

As would be expected, the efficiency of food use by pigs, chickens, wool sheep or dairy cows is better for the higher producers than it is for the lower producers which have higher maintenance costs per unit of production. Most of the investigations upon which this statement is founded have not, however, taken account of the food costs of maintaining breeding stocks. Notwithstanding this lacuna in knowledge, a positive correlation between efficiency of food use and output is one of the chief arguments for intensifying livestock production. Apart, however, from the consideration that net profit is not the only thing to be desired (in a hungry world output per acre would certainly be more popular) the intensification of farming processes is the only open-ended policy, that is, a policy of unlimited future. Those who would seek net profit under conditions of inefficient food use can certainly not hope to increase net profits very far by accepting inefficiency. They cut themselves off from the possibilities of exploiting brains, machinery and land.

Another aspect of the efficiency of food use arises from the sex dimorphism in the size of animals. It is well known that uncastrated mature males of cattle, sheep and pigs are approximately one and a half times as big as the females of the species. The rate of growth of males is faster than that of females, and their efficiency of food use should also be greater. For this reason, to say nothing of reducing pain and encouraging lean meat production, castration may be increasingly regarded as anti-social.

Because of their need for roughage, ruminants are less amenable than pigs to the recording of food consumed. That there will be differences in efficiency among them, however, is not to be doubted. Whether these will be found with respect to proneness to lay on fat, growth rate, milk production, rumen flora or appetite level, is a question for the future to answer. It is also a moot point whether efficiency in milk production, and, particularly, in the protein fraction, has anything in common with efficiency in meat production. Not surprisingly in the circumstances, much of the variation among animals in efficiency is unwanted and has

unknown sources. Even dairy cows still present many problems concerning both the aims of breeding and the methods of reaching them (Lush, 1960). The present organisation and methods of animal breeding are not designed (except in the poultry industry) specifically or effectively to increase animal protein production. There is a regrettable lack of information about the most efficient ways of producing protein. The inter-relationships of breed, body size, feed levels and food composition are likely to be complex but will have to be determined for intelligent production.

The dairy cow is a case in point. Her breeding is often more highly organised than that of any other form of livestock except poultry, and she is a very important source of proteins as milk and meat. Unfortunately, there are no quick and cheap methods of measuring her breeding value from this point of view, and she continues to be selected for type, milk yield, and butterfat percentage. For discussion of the complexities of the genetics of milk protein production and its relation to butterfat production, Robertson, Waite, and White (1956), and Berge (1963) should be consulted.

TABLE 2.4

Apparent digestibility of organic matter of foods by different species in relation to fibre content of food (from Blaxter, 1960)

Species	% fibre 0	15	30
Ox	86	75	63
Sheep	89	76	63
Pig	94	70	46
Hen	86	57	27

If the battle between food production and human reproduction (Luck, 1957) proceeds as predicted, the proportions of the different kinds of animals raised may have to change. Species differ in ability to digest food. Table 2.4 shows how increasing amounts of fibre reduce the apparent digestibility of organic matter far more in pigs and poultry than in cattle and sheep.

Pigs and poultry which have simple stomachs and prefer concentrated food similar to that of man, may eventually suffer in competition for food supplies with him. Ruminants would appear to have good long-term prospects of maintaining or increasing their numbers because they

eat fibrous foods and can make protein with the aid of their microflora out of foodstuffs impossible for man to digest. Thus in spite of the fact that in the ruminant, only 50–70% of the metabolisable energy of food is available, whereas in monogastric species the comparable figure is 80–90% (Mitchell, 1964), they are in no danger of being eventually set aside in favour of pigs and poultry. If the horizon, for policy purposes, is brought closer, the prospects for applying the financing, breeding, husbandry, and sales methods of the poultry industry for the improvement of larger animals are probably better for pigs than for sheep or cattle. Pigs have not only a much higher reproductive rate and therefore higher potential selection differentials, but also have already gone part of the way to achieve the necessary testing facilities, intensified husbandry and simplified objectives.

As Table 2.5 shows, the ox, pig and hen differ from each other in efficiency of gain on any one kind of food, but they do not maintain the same relative efficiencies from food to food. From this particular point of view the best use to be made of food of high energy content and low fibre is to feed it to pigs and hens. However, as demonstrated by the prices paid for intensively reared beef, the laws of supply and demand are quite capable of overriding this biological consideration.

TABLE 2 5

Comparison of species with respect to net energy values of different feeds (from Blaxter, 1960)

Feeds	Absolute values kcal energy gained per gram dry matter			Relative values		
	Ox	Pig	Hen	Ox	Pig	Hen
Maize grain	2 04	3 01	3 05	100	147	150
Earthnut cake	1 77	2 61	2 28	100	147	129
Wheat bran	1 50	1·71	1 06	100	114	71
Wheat chaff	0 63	0 28	—	100	44	—

Considerable changes might be possible with sheep. A ewe normally milks only four months, and the milk is usually converted into lamb instead of directly consumed by man. While she is milking, a ewe is also producing wool that could, if necessary, be reduced and replaced by synthetic fibre. Under such a change in objective, the Wiltshire breed, that produces little more than enough wool to protect itself, may become important.

Like other animals, a lamb is most efficiently growing when growing fast. Since the average growth rate of about 0·75 lb/day is well below that attainable by some lambs, there would appear to be room for improving both mothers and offspring. The cost of production of protein (which amounts to about 5 lb in a 40 lb carcass) in lambs includes the maintenance of a ewe. Hence, it is natural to wonder whether there is opportunity for improvement by (a) reducing the size of ewe, (b) increasing her fertility, (c) improving pre- and post-natal environment to give lambs a quick start, and (d) reducing mortality. Stratified cross-breeding already does much in these directions and could probably do more by emphasising the reproductive qualities on the female side of a cross and growth rate, and carcass quality, especially meatiness, on the male side (Rae, 1964).

TABLE 2.6

Annual feed requirements of ewes and lambs for production (from Wallace, 1955)

	Feed consumption (lb T.D.N.)			
	Weight of lamb in lb	Per lb carcass weight of lamb	Per lb protein in lamb	Per 1000 calories in lamb
Ewe with 1 lamb	77	18·5	149	14·8
	112	14·9	134	9·4
	141	13·8	137	7·5
Ewe with 2 lambs	130	12·8	99	11·6
	192	11·0	95	7·7
	284	10 5	104	5·7

Interesting estimates of the feed cost of producing lamb meat have been made by Wallace (1955). The figures in Table 2.6 have been extracted from his data. These figures show the advantage of twins in lowering costs of production, but also demonstrate how expensive animal protein is in terms of total digestible nutrients (T.D.N.). Table 2.7 shows that lamb, pork and beef compare unfavourably with milk and eggs in this respect.

Demand for more productive sheep to match the increased output from pastures and rising cost of labour and for types specially adapted

for intensive production in sheep houses is focusing attention on breeding for higher fertility, year round lambing, good appetite, and appropriate carcass quality All these objectives seem achievable in the near future in terms of crosses between two or three specialised breeds Lengthening the breeding life of ewes, however, although it would by itself save feed, reduce costs of depreciation and release more young females for immediate consumption, is less promising as a genetic proposition, because of the low heritability of this trait (Bayley *et al*, 1961) and its dependence on fertility

TABLE 2 7

Milk, meat and eggs produced from 100 lb feed and ratio of protein produced to protein in the feed (adapted from Ellis, 1964)

Product	Total product	lb protein in product / lb protein in the feed
Milk	105 0	25
Eggs	32 7	25
Broiler	44 4	22
Turkey	28 7	16
Pork	27 7	14
Beef	12 5	10
Lamb	11 5	08

Total product expressed as live weight or whole egg or milk and protein expressed as edible

In Italy and France the improvement of milk production from ewes is an object of testing and recording schemes and it could happen that, although the breeds concerned are maintained primarily for milk production what is learned from them may influence the thinking of breeders concerned with lamb production For the future, ewes may be needed which have higher milk yields and shorter lactations so as to obtain fast growth in lambs during the first month of life For a review of the quantitative aspects of milk production in sheep, Boyazoglu (1963) can be consulted

Finally, it may be noted that cattle and sheep, as well as pigs, still leave much to be desired with respect to their fertility and viability Although apparently not highly responsive to genetic selection, these traits are economically important Death rates up to 30% occur between birth and age at slaughter and good sense dictates that ways be

found of keeping these losses down. Something more can be done to reduce these losses, including the use of appropriate breeding systems.

B. Improving breeding methods

Although the principles of population genetics are well explored, the genetic details have not necessarily been filled in for the larger domestic animals. For obvious reasons, the study of inheritance has been limited to traits which are commonly recorded and, on a smaller scale, to those observed in specially selected herds. The result is that information about pigs and chickens is more extensive than about beef cattle and sheep; that among dairy cattle, more is known about inheritance of milk yield than about the genetics of its composition; and that in all countries there are breeds about which nothing specific is known. Serious attempts to improve them require an increase in selection differentials, and this, in turn calls for groups of animals larger than normal-sized herds. Furthermore, reduction of intervals between generations and application of performance and progeny testing when appropriate are also required.

Breeders have been often urged to reduce as far as they can the number of traits on which selection is based. Very uneven attention has been paid to these suggestions so far, but the trend is towards their wider acceptance. Oddly enough, it is the so-called practical breeder who shows reluctance to increase the directness and efficiency of his methods. The state of affairs in sheep breeding in the United States has been described by Terrill (1958) in a review of fifty years of progress in sheep breeding research. The growth of scientific knowledge is documented by him and due reference made to the creation of new breeds, but no evidence of genetic improvement in old ones is or could have been given. Instead, Terrill mildly observes that "Commercial producers of wool and lambs sometimes seem to be more aware of the need to apply selection pressure on production traits than are ram breeders and purebred breeders." The same could be said in most if not all other countries.

Although one cause for inefficiency of present-day selection procedures stems from the fact that unimportant selection criteria are often employed, another lies in the use of indirect methods. The time may be soon coming when it will be necessary to pay attention to some traits that are at present ignored merely because of the difficulty of measuring them. Temperament has much to do with the performance of domestic animals. Yet it is very difficult to reduce variation in this character to some scale of values which can be handled statistically, although many studies on genetic determination of temperament in

laboratory animals are in progress (Fuller and Thompson, 1960). Another most important characteristic that is as yet difficult to measure in larger animals is disease resistance. The bases of disease resistance are not well understood but when they are, adequate methods of measuring them will, no doubt, be developed.

For the time being it is true that efficiency of food utilisation in meat animals can best be studied in terms of growth rate, but this stage is probably not permanent. In the future it should be possible to distinguish the various causes of inefficiency. To be able to detect differences quickly and easily would end the present necessity for long periods of recording of consumption which limits the number of animals tested. It is to be hoped that sooner rather than later some connection will be found between observable or readily measurable biochemical traits and metabolic processes that have a demonstrable connection with performance. Because of the comparative ease of controlling their environment and studying very large numbers, it is likely that these developments will take place first with chickens and only much later with such large animals as cows. One example is provided by the study of Wilcox, Van Vleck and Shaffner (1962) of the apparent relation between the level of serum alkaline phosphatase and egg production (see Chapter 9).

Carcass quality, including flavour, has so far proved very resistant to description in quantitative terms. Slight variations important only to comparatively few educated palates should not be allowed to divert research effort from the important problems of learning how to recognise animals of superior efficiency as protein producers and how to manage them properly. This includes testing preconceived ideas about correct conformation to see whether they help or hinder these objectives.

The process of adapting animals to their intended purpose has always been steadily changing and is likely to continue so. Development of techniques for pre-digesting or tenderising meat with papain or other enzymes could have a great influence on the quality that is required in carcass meat. Changes in consumer preference for the amount of fat in meat and their consequences are well known. At the present time, the tendency is away from fat, and, since protein and not fat is in short supply, it seems likely that for the foreseeable future the trend will be in the direction of more protein and less fat in meat. From the same argument it could well be inferred that, provided adequate cheap methods for measuring protein in milk are evolved, the process of changing the composition of milk in the direction of higher protein content would receive impetus. The slaughter of young animals for meat, to have them tender and free of fat, could be reversed by advances

in meat technology if it proves possible to treat meat to conform to public taste without killing animals at very young ages. This would require alteration in selection procedures, so that animals would be bred to reach their maximum economic protein production at greater ages, in order to reduce the overhead costs of maintaining breeding stock by producing a greater amount of meat from each of their progeny.

Technical developments create new problems but they also make some old ones irrelevant. For instance, drugs for disease control have altered the importance of resistance to worms, footrot and blow fly in sheep. Better understood mineral requirements have made possible the prevention of some metabolic diseases. New ideas in housing and in husbandry, however, are likely to bring new breeding problems in their train, because of the changes they involve in lighting, in the introduction of heavy feeding, of damp atmospheres, and of closer social relationships among animals which were free to avoid each other under the old systems. The ambitions of those who would breed better animals and of those concerned with their husbandry are thus mutually interdependent, and call for advances in methods of controlling both nature and nurture.

By intensifying animal production on land that will permit it, or in buildings, the need for locally adapted races might be reduced. Much will depend on the reasons for having local races. Requirements for adaptation to local markets or local diseases may or may not be changed much, but ability to stand a harsh climate or inadequate food might no longer be an essential. The dense housing of poultry, for instance, has brought in its wake a new set of health problems and the development of appropriate counter-measures. Performance testing of pigs on feeding systems capable of maintaining very high growth rates has also brought problems such as watery meat and foot weakness. With this experience as a guide, it would be wise to prepare to deal with nutritional and pathological issues in housed sheep as well as with those in swine and cattle. Much attention is being given to what have been called the emerging diseases (Food and Agriculture Organisation, 1963) that are spreading to new territories or increasing in frequency as stock rearing becomes more intense. There is, however, a long way to go before the collaboration of veterinary, nutritional, genetic and other specialists accords with the need. Such machinery as exists for collecting appropriate research data on these several aspects of Johne's disease, enterotoxaemia in sheep, and blue tongue is pathetically inadequate, and these are only three of the more important and worsening diseases.

As man's control of animal environments grows more efficacious, differences in husbandry practices will shrink. In tropical countries anxious to enjoy the benefit of livestock of high productive capacity

from temperate regions, there is every reason to hope that the control of environment, which now permits modern poultry keeping, can be extended to other classes of stock, especially dairy cows.

Most discussion of livestock improvement centres on the aims and methods of selection processes applied within breeds. As such it is only tactical in scope. On the strategic level, a hypothetical high command would concern itself with selection between breeds, and the relations between dairy cattle, beef cattle, pigs, sheep, chickens and turkeys. What producers spend on their own development is their business, but the amount of taxpayers' money to be spent on advisory and research work aimed at increasing productivity is apparently not governed by any known set of principles. These six sub-industries are competitive in this respect as well as in food markets. Those prepared to help themselves, especially poultry and dairy cattle, have shown advances in efficiency and production to repay efforts put into research and development. No doubt sheep and beef cattle could do likewise. But it is perhaps debatable whether scarce resources of advisory and research personnel should be diverted to improving them if the breeders do not wish it. However, should improvement be in the public interest, breeders cannot be allowed to impede it while demanding protection from competitors.

Although it might be possible to compute a regression function relating improvement to expenditure on development as a useful guide for those who have to decide on the amounts to spend on conflicting claims for assistance, such a function cannot be devised for basic research. This means that many research projects must be supported in order to make sure of supporting the few which turn out really valuable in improving current breeding methods. A further discussion of this problem is contained in Part IV.

breeders nor geneticists have developed any close collaboration with economists with a view to finding out what are the greatest economic weaknesses of the various breeds available. Selection indexes need realistic economic values not now available. The economics of breeding, including the cost of improvements and their value, ought to be known, no matter whether carried out by breeders or large organisations as a hobby, for a living, or as a public duty.

The making of new breeds is a sign of virility in agriculture and is to be welcomed. Those who embark upon such a venture, however, should remember the lessons of history and make sure that their stock is not left to speak for itself. Advertising is not a substitute for performance but in our society it is an essential complement. Promotion nowadays usually begins when, or even before, a new breed is started. This sometimes applies also to a proposal to import a foreign variety. By the time there is a sufficient surplus to permit sales, much has been done to create the impression that there is a need for new stock of high performance. Since at least some importations have much merit in their home lands, the claims made by promoters of new breeds are quite likely to be justifiable in some sector of the livestock industry. No objective trials of new breeds are routinely encouraged anywhere, and therefore the testing of these claims is usually a prolonged and chancy empirical process that could easily be replaced by a formal and adequate procedure sponsored by a progressive industry.

There is no genetic difficulty in making a new breed. Such problems as there are arise from promoting it. Sometimes it is an advantage to have a recognisable type as, for instance, in polled versions of horned breeds or crossbreeds, especially if recognition by Government inspectors is required, as it is in Britain. The official commending of colour-marked cattle helped the Hereford and Angus breeds. A new breed with a dominant trait would have a corresponding advantage by advertising its use in crossbreds as well as purebreds. Where, however, it is desirable from the promoter's point of view to limit multiplication of his breed to his own stock, a recessive colouration is preferable since it would disappear in at least some crossbreds. These elementary considerations are no longer of interest in the highly integrated poultry industry but they are still important in cattle and sheep breeding.

New breeds have been justified on at least two grounds. Firstly, there may be economic and environmental niches to which existing breeds or crossbreeds are not well adapted, or could not easily and quickly be adapted. Numerous creations of this kind have been successful, including the Lacombe pig, Corriedale sheep, and Santa Gertrudis cattle. Although extreme examples might be convincing, objective assessment

of the case for a new breed as an alternative to improving an existing one is usually impossible.

Secondly, some useful genes may, for practical purposes, be absent from one breed and become available only by starting a new breed on a crossbred foundation, as has been done several times in order to produce polled varieties of cattle. Sheep suitable for year-round breeding might be best designed with one of the recognised breeds of extended breeding season as a component. No one knows, however, how much genetic variation there would be in standard breeds if they were given the chance to show it, nor, therefore, how easily they would be modified by selection. How much more or less effective selection within an existing breed would be than selection in a new breed of crossbred origin is usually a rather academic question. The real reason for the making of new breeds is that it is difficult to attain effective selection within an existing breed. There are several explanations for this. In some countries breed structure may be too ill-defined to serve as a basis for a concerted effort. In others, the restrictive practices of breed associations which are thought to be essential to survival preclude too much enterprise among members. One type is made official and any other is frowned upon. What perhaps should cause anxiety is that breed associations might learn the risks attached to forcing progressives to set up rival associations, and may smother them with kindness within the family. In genetic terms, the rate of improvement may be greater if sought in inter-breed rivalry than in intra-breed orthodoxy.

Although many experts in the past have been willing to announce beforehand whether or not a new breed or sub-breed will be economically desirable, necessary, or potentially useful, there is, in reality, no way of knowing. Since impartial and comprehensive evaluations of whole breeds are not available, none of the existing, let alone new ones, can be classed as necessary or unnecessary. In brief, the value of a breed lies in the minds and ambitions of the owners. No conditions for success or failure can be laid down but several with a bearing on the outcome of

which still requires genetic diversity and selection for consequent change. Animals, whether wild or domestic, which have ceased to evolve have as a rule begun the downward path to extinction. Darwin came to this conclusion a century ago and there seems to be no reason at present to come to any other for domestic animals.

V. Unorthodox Food Sources

Pirie (in Royal Statistical Society, 1963) suggests that some species of plants and animals not now utilised to a great extent in human nutrition could be exploited for that purpose. Such species must be acceptable as foodstuffs and must not compete for energy sources with man or with current links in man's food chain. More extensive use of horse and dog meat could be encouraged in the West, but because of the kind of food these animals require they cannot make much of a contribution to the solution of the problem. There might be some judicious harvesting of wild animals (Ovington, 1963). Granted that venison, grouse, pronghorns and many other species are now being cropped, there is still a great number of relatively unexplored possibilities. For instance in an economic study carried out on an African ranch (Dasmann, 1964), it is claimed that on a given area, presumably capable of producing an annual yield of 94,500 lb of beef were it devoted to this purpose, 118,300 lb of game meat might be obtained by providing a little protection from predators and some careful culling. Other suggestions for harvesting wild animals are shown in Table 2.8.

Game ranching seems to have something in common with sea fishing. But as yet it has neither the capital investment nor the skilled labour. It has also to learn how to live with migrations, epizootics, droughts, fires and predators. As Dasmann (*loc. cit.*) puts it, the argument for game ranching in Africa, as in the United States, is that it is a means towards conserving the fauna. Well established wild populations, like domestic ones, can tolerate and even benefit by periodic reduction of numbers and if, in the process of conservation, some financial return through shooting licences or sales of meat is to be had, so much the better.

Texas for raising on marginal land unsuitable for cattle grazing). It is probably not far from the truth to say that the ratio of the number of species of animals used as a source of food to the number of known species is not more than one to three or four thousand, and this ignores the relatively unused potential of sea farming.

TABLE 2.8

Yields of wild and domestic animals (from Pirie in Royal Statistical Society, 1963)

Type of land	Measure of yield	Domestic animals	Wild animals
Range	Kg live weight/animal/day	0·14	0·19–0 24
Savannah	Kg live weight maintained/hectare	20–28	157
Bushland	Kg live weight maintained/hectare	3·7–13·5	52·5
Chernozem	Animals/mile^2	34	134
Depleted land	Kg live weight/hectare	15·5 (further depletion)	31 (recovery)

As Reed (1959) and Zeuner (1963) explain, the origins of domesticated animals are remote and exceedingly vague. The behaviour patterns of man having changed in the meantime, the study of domestic animals today is a most uncertain approach to the circumstances in which domestication was brought about. Some arts, now little cultivated, but based on imprinting or other facets of animal psychology may have been practised widely in the distant past. Domestication is not likely to have been of a once-for-all nature and modern ethology may help to mark the end of the second millennium A.D. as a notable era in this process.

In addition to harvesting what may be called sea-crops in the form of protista, crustaceans, fish and mammals (extensively documented in Ovington, 1963), intensive artificial culture of fish has recently come into prominence in Europe, Asia and Africa (Hickling, 1962). There seem to be exceedingly fruitful potentialities in replacing haphazard fishing methods by stock-raising in ponds of a great variety of species of fish, either directly edible by man or usable as a protein source for conversion into beef or poultry meat. The food chain in the latter case, although relatively long, would not involve competition between man and livestock. Indeed, intensive attempts to establish efficient selection schemes for improvement in yield and quality are already under way (see Wohlfarth *et al.*, 1965).

Although the food reserves in the salt seas seem comforting, it is well to remember the potential difficulties in using them. Apart from technical problems, including management of hatcheries, use of fertilizers, and control of predators and competitors, that are as yet unsolved, there is the prospect of international rivalries of the kind that make the future of whales look bleak.

With land animals, it may be a question as to how appetising zebras, steenbocks, kudus, impalas or other similar species would be to urban populations. Indeed, the human palate, at least in short-range terms, may prove to be a severe limiting factor in utilising other untapped animal resources. People tend to choose foods rather than nutrients and their choice is conditioned by racial and other prejudices, rearing, religion, and magic as well as by availability and attractiveness (Campbell and Cuthbertson in Cuthbertson, 1963). It is not impossible to influence the diets of those who habitually suffer qualitative deficiencies but it will often be a long task. Pirie (1962) has emphasised this point after presenting a long catalogue of such potential contributors to the dining table as the capybara, the kangaroo, the hippopotamus and other aquatic mammals, the guinea fowl, various reptiles and amphibia, fresh water and marine fish not currently used on a sufficient scale, and invertebrates including snails, locusts and larvae of various insects. It should also be noted that these and many sources of vegetable protein such as Pirie's (1958) leaf extract, that are for the time being unacceptable to man, could still find utilisation in livestock feeding.

Welcome as new sources of food from land animals would be, there is no apparent prospect that any of them could relieve much of the world's needs of animal protein. It is necessary therefore to consider what can be done to raise production from existing livestock industries. Much effort is properly being applied to questions of health, nutrition, and food preservation. In this book, however, discussion is limited to matters arising primarily from the genetic aspects of animal production.

Part II: The Theory of Animal Breeding

CHAPTER 3

GENETIC THEORY

The foundations of modern genetic theory were laid by Mendel in 1865. He was successful because he chose for experimental breeding, probably on the basis of *a priori* deduction, contrasting characters that were simple, easily recognised, and, in modern terms, very highly heritable. He suggested that his pairs of alternative characters were essentially controlled by corresponding pairs of "factors" in the parents, and that in the production of a fertilised egg one of each pair of factors was contributed by each parent. Subsequently, his factors became known as genes, and their physical nature and mode of transmission of genetic information from ancestors to descendants established. Particulate theories of heredity were not new, but this one, involving pairs of alternative factors, explained the regularities of inheritance which Mendel observed. These regularities are now enshrined in Mendel's laws. Their existence has provided a mathematical basis for predicting results of matings and for testing the laws in a great variety of animals and plants under all manner of conditions. During the past century no multicellular animal or plant has been found to ignore them entirely. Abundant exceptions, deviations and complex combinations of them have, however, been found.

After investigating what at first appeared to be failures of the laws, geneticists have modified and extended them. A body of genetic theory is therefore now available which, although by no means explaining everything, does remove much of the mystery from animal breeding and provides a far better foundation for action than was formerly available.

Population genetics is a logical development from these basic principles of inheritance and variation. It attempts to describe in algebraic terms the results of transmission of genes from generation to generation and to predict the behaviour of future generations in enormously more intricate situations than those considered by Mendel.

Whereas Mendel worked nearly entirely with a few genes with clear-cut effects, the population geneticist often extends his studies to genes the individual effects of which are often too small to be discerned. With the aid of computers and appropriate algebra, he can work out the consequences of his hypotheses and test them on large populations whether real or simulated. Fortunately, much of the research that produced the theory behind population genetics originated from livestock data and, consequently, there is no dearth of evidence that the theory goes far to account for the variation in populations of animals.

During its history, genetic theory has had to accommodate new facts as they were revealed. This process has not ended. In most characters of livestock that are of high economic importance there is always a large part of the variation which is not attributable to any specific genetic or environmental cause and this part is vaguely called environmental variance. When the heritability of milk yield is stated to be 25%, it is implied that variance of non-genetic origin (or genetically non-additive) is 75% of the total. Some of this, as twin research shows, is attributable to season of calving, inaccuracy of observation and other specific factors, but much is still unaccounted for. It is eminently possible, therefore, that this fraction could be found to contain variability among cows due to the interaction between heredity and environment, that is, due to a varying response to varying challenges from pathogens, mineral deficiencies and other unrecorded items of the environment It is possible (but not yet demonstrated) that breeders of cattle might occasionally recognise some such interaction and, by acting accordingly, attain better results in a particular herd than would the approximations of genetic theory. Better results will also be due sometimes to chance.

Under most practical circumstances there is no incompatibility between efforts to exploit genetic variation by selective breeding and efforts to remove some of the environmental variation. It is sometimes urged that because the latter is for many important characters relatively large, attempts to eliminate it would offer better prospects of improvement than selective breeding. Certainly, if performance can be economically improved by altering some aspects of management, it would be intelligent to do so, although not necessarily intelligent to ignore heredity at the same time Unfortunately, the causes of environmental variation are often unknown and therefore not easily removed. Some are known (for example, age or season) but cannot be eliminated. In the best-regulated herds of dairy cows, environment accounts for about 75% of the variation in lactation yield. At present, there is remarkably little that practical breeders can do about it. This state of

affairs, no doubt, will gradually yield to research and, as it does, the heritability of milk yield will rise and with it the efficacy of selective breeding.

Twin research with cattle has already shown how this may come about. The extraordinary similarity of identical twins, not only in colour and form but in growth rate and milk production, turns out to be due not only to their genetic identity but also in part to the reduced range of environments that most twin experiments afford (Donald, 1959). Because twins are housed together and fed alike, all the physical and other external variables on a farm which a given pair experiences, provide only a limited sample of possible environments. Not all characters are equally affected by this uniformity of experience. As might be expected, live weights at 18 months of age, which sum up the preceding nutritional experiences of a pair of twins, are more influenced by season of birth, plane of nutrition and juvenile diseases than are the numbers of services for successful conceptions just at that age. Experimental control thus achieves more for the former than for the latter.

I. The Genetic Basis of Animal Breeding

It may be appropriate at this point to examine the major assertions and postulates of animal breeding theory upon which the genetic approach to animal improvement is based. Fundamentally, they are rooted, as has been stated, in Mendelism, as extended (with a few exceptions of straight-forward traits controlled by single genes) to polygenically determined characters. The following account is semi-technical and is not essential for many of the subsequent chapters. Readers who wish more information on the subject are referred to several books available in English including those by Lush (1945), Mather (1949), Li (1955), Lerner (1958) and Falconer (1960). Those whose interest in the technical aspects of genetics is limited, and those intimidated by the specialised vocabulary should omit the remainder of this chapter.

Perhaps the first few of the basic formulations to be presented are by now commonplace, and will be taken for granted by most readers acquainted with genetics. Nevertheless, it may be well to devote some space to them, since subsequent statements, which may not be as generally accepted, are extensions of them.

To start with, it must be said that non-Mendelian inheritance, such as that based on the transmission of cytoplasmic particles, has so far not been shown to have much significance in animal improvement. Although evidence on possible cytoplasmic effects have been reported for domestic animals (e.g. by Allen, 1962, for chickens), it appears to be

of a tenuous kind. This is not to say that differences between reciprocal crosses due to maternal effects are of no importance, nor is it to deny the role non-genic (cf. Sonneborn, 1964) or non-chromosomal material (Sager, 1964) may play in genetic processes.

A rejection of the claims for what has been called by the Lysenko school vegetative hybridisation of animals seems to be needed. A voluminous literature has accumulated which attempts to present a case for the possibility of transforming hereditary endowment of animals by such techniques as blood transfusions or by exposure to foreign genic material (DNA). But the results of the best controlled experiments on the subject (Buschinelli, 1961; Burger, Shoffner and Roberts, 1961; Kosin and Kato, 1963; Billett, Hamilton and Newth, 1964) were completely negative. Yoon (1964) attributes the failure of the experiments in which DNA was used for the attempted transformation to the low rate of its incorporation into recipient cells. Since in his tests on mice, the injections were not only of homologous material, but also intragonadal rather than intra-peritoneal, as in some allegedly successful transformations, the interpretation of the latter has to be made even more cautiously. The most that can be said of the positive evidence presented in publications emerging from other than Eastern Europe (those by Benoit, LeRoy, Vendrely, 1958; LeRoy, 1962; and Stroun *et al.*, 1963), is that indications suggesting the utility of incorporating these techniques are not ready for use in improving livestock.

Before proceeding with a more formal exposition of the accepted principles of animal inheritance, a reference to the recent developments in genetics, deriving largely from work with lower organisms, is called for. The units of various kinds of genetic function, such as cistrons, mutons, recons, or the more recently suggested polarons, as well as the concepts of modulators, of operator, regulator and structural genes and controlling elements in general, the relationship between hormones and genes, the phenomena of position effect, paramutation and gene conversion, which are being built as a superstructure on simple Mendelian theory (see e g. Stent, 1963, Herskowitz, 1965, and other modern textbooks of genetics) are of undoubted great significance in understanding the working of the hereditary apparatus. It is true that analogies between these mechanisms in bacteria and in higher organisms (e.g. control of haemoglobin structure in man) have been proposed, but these aspects of the newer genetics have not yet made an impact on the breeding of domestic animals. There is a need to undertake and expand genetic studies of chromosome aberrations, so actively pursued in man, and of cell activities on a molecular level in economic animals; for the present, however, the postulates underlying genetic improve-

indicate that linkage disequilibrium can have significant effects on selection results.

5. *All phenotypic differences between individuals are determined by genetic factors resident in the chromosomes and by environmental factors resident outside of the chromosomes themselves, as well as by interactions between the two types of determinants.* Under this definition cytoplasmic and maternal effects would be classified in the environmental portion of variability. The interactions may arise between genotype and location, and between genotype and year or generation. Individuals or inbred lines tested for performance at one station may rank differently at another or at the same location at different times. The switching may be due to variation in climate or other external environment or to variations in the internal environment of the animals themselves (for instance, immunological reactions to subclinical diseases and infections).

6. *Genotypic variance is divisible into additive and non-additive portions.* The first of these consists of variability contributed by additive effects of genes. This is the portion which will contribute directly to selection progress. The second type of variability is produced by interaction between genes. Interaction between alleles, that is, dominance effects, may fall into one or the other category depending on gene frequency. Effects of over-dominance and interactions between genes at different loci which may be grouped under the general heading of epistasis are non-additive. This postulate is of considerable significance in selection theory, since prediction of advances under selection depends on Mendelian algebra addressed to the additive variability.

7. *Environmental variance is divisible into a portion common to the whole population under observation and a portion which may be common to some members but not to all members of the population.* A simple example is the maternal effect which offspring of the same dam share but which does not contribute to the similarity between half-sibs by the same sire. Another example is a byre or herd effect, present when the offspring of a given sire are housed or maintained together and thus become phenotypically more similar to each other than they would be from strictly genetic considerations.

8. *The mean additively genetic value of a population depends on gene frequency.* This is simply to say that if differences between genes at a given locus are translated into phenotypic effects, what may be called the expected average merit of the population is merely the average of the sums of such individual effects of all genes over all individuals.

9. *The non-additive genetic value of the population depends (in addition to gene frequency) on the breeding structure of the population.* The diploid combinations of various genes determine the genetic endowment of the individual but not necessarily the genetic endowment of its offspring. Under inbreeding it is possible that more diploids of one particular genotype are present in a population than would be expected to occur in random mating. Similarly, under out-crossing certain other diploid combinations may be found at a non-random frequency. The distinction between the additive and non-additive genotypic value of a population is of fundamental importance in projecting the effects of different kinds of selection. Indeed, it is this distinction that makes those systems of improvement based on heterosis and those based on ordinary additive gene action so different from each other.

10. *A randomly mated large population will in the absence of disturbing pressures maintain constant gene frequencies.* This is the so-called Hardy-Weinberg equilibrium discovered in 1908 or earlier. The process of improvement calls for increasing the frequencies of genes deemed desirable, and, hence, for applying pressures disturbing the equilibrium.

11. *The significant changes in gene frequencies of domestic populations depend on three types of processes: systematic, random and unique.* Since change in gene frequency is the most important contributing factor to the improvement of populations at least at present, this postulate needs somewhat more extended discussion than the others. A comprehensive analysis of the forces entering these processes is given by Wright (1955). Here, factors of significance in domestic rather than natural populations are emphasised. Thus, although in the latter, recurrent mutation is of considerable import, the relatively short-term aspect of domestic breeding populations makes this systematic process only of retrospective significance. Detrimental or deleterious genes may be present in any given population because of recurrent mutation in the past, but in the course of existence of a flock and herd the newly appearing recurrent ones can play only a small role. In other words, the significance of recurrent mutation in animal improvement relates to the elimination of undesirable mutant genes that have previously arisen and to propagation of advantageous ones. But this, of course, is the process of selection. Hence, one may say that among the systematic processes selection is the most important force operating on gene frequency and hence in the improvement of additively genetic traits.

Recurrent immigration which may involve cross-breeding is another systematic process relevant to the improvement of domestic animals. The introduction of new genes and increases in frequencies of genes already present can be obtained by this method.

Classified under random processes are various fluctuations in gene frequency and, in particular, those due to accidents of sampling. Since changes in gene frequency depend on selection or introduction of diploid individuals (even if it is done in the form of importing sperm or by using artificial insemination) there are sampling variations in both selection and migration. Their magnitude may be practicable from knowledge of the population size but their direction cannot be predicted for any particular case. It is clear that the importance of such random processes increases as population size decreases. In one-sire herds, for instance, the effect of chance would be much greater than in a population utilising a hundred or more sires.

The extreme form of this effect may be, in a sense, a unique event. Accidental fixation of an allele may possibly occur if the breeding population is small. In the formation of the early breeds the initial gene pool was a restricted one, so that the genetic variability was severely circumscribed. This situation is very much akin to the evolutionary *founder principle* of Mayr (1957) who describes it in the following words (for "colony" read "breed"): "The founders of a new colony of a species contain inevitably only a small fraction of the total variation of the parental species. . . . All subsequent evolution will proceed from this original endowment. How important this restriction is, is evident from recent selection experiments in which several lines were exposed to the same selection pressure. Almost invariably the end results were different in the different lines." Of other possible unique events, the origin of a mutation novel to the breed, such as double muscle, or the chance selection of an exceedingly good sire at one end of the frequency distribution of genotypes or, yet again, an epizootic which would suddenly reduce the breeding size of the population, may be mentioned.

One more category of modes of change of gene frequency has been considered by Wright. It includes changes in the system of coefficients determining the magnitude of the other processes, changes which occur because the gene pool of the population has been undergoing a transformation or because the environment is no longer the same. In an artificial selection programme it is unlikely that these modes need to be considered independently of the

factors already discussed. However, one point must be stressed here and that is that natural selection continues to produce effects even in domestic environments where populations are subjected to artificial and directed forms of selection. In some instances, natural and artificial selection may work hand in hand, as perhaps, is the case with viability. In others, they may be antagonistic because of genetic homoeostasis (see postulate 16) as in an experiment on selection for long shanks in chickens (Lerner and Dempster, 1951). In general, it must be realised that, while natural selection can occur without artificial selection in the wild, the laboratory or the farm, the reverse is not true: probably all artificial selection (that is, selection imposed on a population by man for whatever purposes) is accompanied by natural selection, which is purposeless and is merely a process involving differential reproductive ability of animals with unlike genotypes (see discussion by Lerner, 1958, 1959).

12. *Heterosis may result when the chromosome complements contributed by each parent derive from populations of different origin.* It does not matter whether heterosis is due to single locus overdominance, to combined dominance at many loci, or to other reasons. From the standpoint of the application of hybrid vigour in animal improvement, the details may differ depending on which one of the explanations for heterosis is correct, but the general principle of producing heterosis by combining gametes of unlike origin is still valid.

13. *Inbreeding degeneration depends on an increased proportion of homozygous individuals in the population, which is the result of severe reduction in effective population size.* Neither the particular basis for heterosis nor *a priori* specification of the characters which will display inbreeding degeneration is included in this formulation. However, speculations on the relations between reproductive traits and characters which are apt to show the greatest effects of inbreeding have been made on an empirical basis among others by Robertson (1955) and Lerner (1958). Further reference to this subject is to be found in the last section of this chapter.

14. *Phenotypic correlations between different traits are the result of combination of genetic and environmental correlations.* Genetic correlations may arise from pleiotropic action of genes, from linkage, or because of common introduction of the genes involved into the population. Environmental correlations are a result of the fact that two or more traits develop in the same animal and are thus exposed to the same environment. This postulate or proposition is

of utmost importance because the theory of index selection, one of the highly significant contributions of population genetics to animal improvement (discussed in Chapter 4), is founded on it.

15. *As a result of selection for one character, correlated responses in others occur.* Empirically, this fact was well known to Darwin but its genetic basis arises from the theory of genetic correlation subsumed in the previous paragraph. Of a special importance in breeding improvement are the correlated responses in reproductive characters which often seem to occur after prolonged selection. Their basis has been discussed, among others, by Mather (1943) and Lerner (1958), and will also be considered in the next chapter.

As a corollary to this and the previous postulate, it follows that secular changes in the values of genetic correlations will occur under selection. In other words, traits which may not have been originally correlated may become correlated (particularly in a negative way) as a result of selection for one or both of them. The practical consequence of this situation is that the parameters which have to be used in constructing a selection index are subject to change whenever genetic correlations appear or change in value (see the section on selection indexes in Chapter 4). In general, whatever deficiencies in practice result from the application of propositions 14 and 15 must be laid at the door of deficiencies in knowledge rather than in their erroneous nature. It has been repeatedly stressed by proponents of population genetics that more precision in determining the various parameters is required. This precision clearly depends not on matters of principle but on obtaining additional information.

16. *Individual genotypes resulting from prolonged selection show a considerable degree of genetic balance.* Further selection in some specific direction, not for total fitness but for traits which may be useful only to man rather than to the animal itself, may lead to deterioration in reproductive performance with a consequent antagonistic action of natural against artificial selection. Suspension of selection under these circumstances may be expected to result in a full or partial return of the selected character to an unimproved level and in restoration of reproductive fitness, provided the inbreeding has not been too intensive. Lerner (1954 and 1958), and Robertson (1956) have discussed the various aspects of this phenomenon of genetic homoeostasis as well as conditions under which it may occur. It should be noted that the empirical facts regarding the regression of characters displaying genetic

homoeostasis are independent of any particular theory or hypothesis (such as heterozygous superiority suggested by Lerner, 1954). Furthermore, it cannot be predicted on *a priori* grounds which characters will exhibit this behaviour unless their relation to reproductive fitness is known. There are examples of highly additive characters which as expected do not show it, but there are also experiments on record in such traits as egg number which, by the time selection becomes ineffective, is very likely based on largely non-additive gene action and regresses relatively little (see the section on selection in poultry).

These sixteen propositions can be put in a still more general form. They can be condensed into four broad contributions of genetics to the techniques of animal improvement:

1. the mathematical model of Mendelian inheritance,
2. prediction of selection gains,
3. heterosis,
4. balance and co-adaptation.

II. Genetics and Improvement

The mathematical model of Mendelian inheritance extended to polygenic characters, and the partitioning of total phenotypic variability into its various genetic and environmental fractions are still the bases of selection in closed or in partially isolated populations. This is true, even though some specific problems have not been completely solved. Optimal or minimal effective population size, for instance, or optimum selection intensity which may depend on whether a short term or long term outlook is considered, need more study.

The theory of prediction of selection gains and hence the possibility of *a priori* comparison of different breeding systems has been worked out. In many ways this still has considerable weaknesses, largely because of the uncertainty about many parameters and the assumptions that have to be made. Indeed, perhaps the biggest problem that technologists of animal breeding have to face is that of finding signals which would indicate that a selection method has reached the point of diminishing returns or at which it is no longer as efficient as some other method. Because of the fact that a good many traits much subject to non-additive gene effects have also high environmental variability, progress in any given population is not easy to check and the approach of a trait to a plateau is not immediately detectable.

There is now an appreciation of the economic possibilities of heterosis and the associated idea of selecting for combining ability, that is to say,

for a high performance of crosses between lines, breeds, or strains. One of the most spectacular transformations which has occurred recently in animal breeding has been the spread of this system of improvement in poultry breeding. But it is predictable that no one system will last indefinitely, for the balance sheet of genetic variability dictates that gains are achieved at the cost of reducing variance. This means that whatever system is used (and the more efficient the system may be, the quicker this will happen), sooner or later genetic variability which responds to this particular system will approach exhaustion, and either new variants or alternation between the known systems of selection and mating will have to be resorted to. Indeed, this is a direct consequence of the fourth and final contribution of population genetics and that is the development of the concept of balance and co-adaptation in Mendelian populations. Essentially, this idea refers to the resistance of an adapted population to change and, in some instances, to the regression of gains under suspension of selection. One of the forms in which this phenomenon expresses itself is the reduction in reproductive capacity following intensive selection for some useful traits. For example, the great increase in the body size of turkeys has been accompanied by a serious drop in fertility.

At the moment, the immediate future developments arising from the principles that have been discussed call for research along several lines. As part of the operational research to be carried out by industry, more precise information on various parameters entering decision functions in animal breeding is required. As part of the operational research by academic institutions, removal of various restrictions on the genetic model must be studied. What is called the Monte Carlo type of investigations of the consequences of selection and mating systems (methods which involve computer-based theoretical investigations of the kinds of outcome to be expected from any system in terms of probabilities) may be suggested. In the same area of research, clarification and validation or discard of the various assumptions that have been discussed might also be listed. Finally, in terms of purely academic or basic research, all of these assumptions, as well as any new ones that may be proposed, should be investigated not only in terms of statistics but also in the light of newer knowledge in molecular biology and biochemical genetics. It is not at all improbable that the newer concept of the gene as a stretch of DNA coded for a protein may call for a drastic revision of mathematical genetics based on the so-called beanbag model of fifty years ago

There is no need to elaborate the points of difference between the foregoing approach to breeding and that which was common before

population genetics developed. Such notions as identity of genotype and phenotype, or, at a later stage, the notion that an identical pedigree implies an identical hereditary endowment, the confounding of genetic and environmental variation, the goal of producing single superior individuals rather than improving the average level of a population, the refusal to use as a parent an individual of unsatisfactory performance but with high combining ability with another parent of equally unsatisfactory performance, are still prevalent among large animal breeders, and all are incompatible with the current concepts of population genetics. The question must, however, be asked whether or not the more modern ideas are an improvement on the old ones. A number of experiments have addressed themselves to this problem. Most of these have been carried out on laboratory animals in pilot experiments, largely because of the length of time and the high cost which experiments on economic traits would require. But some indications are available with respect, firstly, to the validity of the general ideas of polygenic inheritance based on the Mendelian scheme and, secondly, regarding more specific agreement or lack of it with prediction on the basis of the propositions that have been listed earlier. The literature on the subject is exceedingly large and it would serve little purpose to attempt a full discussion of it here.

With regard to laboratory animals the reader may be referred to the reviews by Chapman (in Hodgson, 1961) and Kojima and Kelleher (in Hanson and Robinson, 1963), who have considered *Drosophila*, *Tribolium*, mice and other laboratory animals that have been used for experiments on selection and the general principles underlying such studies. In general, what emerges from the results is that, whereas in many cases prediction of exact gains from a theoretical consideration of the methods followed departs considerably from the actual results, the selection methods whether they be individual, family or for combining ability, are appropriate where theory so indicates. But, generally speaking, for short terms, that is to say, several generations, the realised results of given mating and selection practices do not seem to vary greatly from what is theoretically expected. Furthermore, a good many of the possible reasons for discrepancy between expectation and actual results have become evident as a result of such experiments and are being further checked. Opinions dissenting from this generalisation (e.g. Sheldon, 1963) should, nevertheless, be noted.

III. Verification of Selection Results

In larger animals this problem is more complex. The issue whether or not there is adequate evidence that genetic principles work in livestock

or poultry has been often raised. It has proved difficult to obtain precise and useful information on this point. Indeed, it is rarely an easy matter to discriminate between the great variety of explanations that may be advanced for changes in performance observed over a period of time.

Perhaps the best that can be done is to consider each individual case after generalisations as to the effectiveness of alternative breeding systems have been reached. Thus, if it can be established that with respect to, say, litter size in mice, a particular system of selection is entirely inadequate, it might be concluded that for pigs the same system is not likely to have been responsible for whatever results occurred in the course of its use. Such an attitude may not satisfy everybody. It does point strongly to the necessity of continued experimentation and of further accumulation of data on this matter in a variety of species. The difficulty is that experiments which might lead to conclusive results are exceedingly elaborate, expensive and require a long time with all but very short lived animals.

A number of considerations relevant to tests on genetic improvement can be set out without even mentioning staff, facilities, time and cost. In part, the discussion of this matter has been adapted from the review by Chapman (in Hodgson, 1961). However, his ideas have been expanded and somewhat modified in what is to follow.

Firstly, any experiment aiming at conclusive results must have adequate population size and a number of replications of whatever procedures are being tried out. In the past this has been a crucial defect in most work dealing with larger animals. Indeed, it may be questioned whether the expense and effort involved in meeting these requirements

comparable to that which the animals would eventually encounter in the field might have to be provided. There are so many intangibles even in a "constant" environment for larger animals (for instance, uncontrollable variation in quality of food, day by day or year by year) that to meet this requirement fully is probably out of the question. Finally, the keeping of accurate individual pedigrees throughout the experiment is clearly necessary.

Various kinds of information must be collected in order to have a chance of interpreting the results. At least ten may be mentioned irrespective of the character under selection. It must also be kept in mind that in most situations of interest to the animal breeder more than one character is used in selection. This fact introduces tremendous complications that make the recording of the necessary data very cumbersome.

1. *The kind of selection used.* That means determining the exact emphasis placed on the individual, the pedigree and family, be they sibs or progeny, and also on the various aspects of performance.
2. *The mating system.* The results will depend on whether the mating of selected animals is at random, whether like are frequently mated with like, whether inbreeding, out-crossing or back-crossing to a superior individual is practised. There are some complications here with many large animals in quantifying precisely what has been done. In pilot experiments with mice or fruit flies it is often possible to set up a rigid system of mating, such as mating only double first cousins. In such large animals as cattle, however, this becomes very difficult because the correct mates may not be always available when they are needed.
3. *The extent of inbreeding.* This is normally possible to compute, at least in theory, from the pedigrees and often from the nature of the mating system. The actual increase in homozygosity which is the really interesting information is usually not available. In *Drosophila* it is possible to approach the answer if suitable "trick" stocks are used, but there is no immediate hope of utilising such methods in the larger domestic animals (see the section on trick breeding in Chapter 4).
4. *The amount of selection attempted and realised.* It is of vital importance to know how much selection pressure is being applied, that is to say, how superior the animals used for breeding are to the other animals of their own generation. There are different ways in which this superiority may be expressed. It could be shown on a phenotypic scale as the performance of the individual animals selected relative to the average of their generation. With

sex-limited characters this cannot be done in one of the sexes and a scale based on progeny test or family record has to be used instead. Sometimes a selection based on pedigree has to take into account the superiority of the immediate ancestors. In addition to the specification of the amount of selection applied, it is necessary to know whether in fact the attempt has been successful. It may happen that the artificial selection pressure is interfered with by a counter-pressure of natural selection so that the breeder over-estimates the actual amount of selection applied. He might choose the top 25% of his population for producing the next generation, but find that the very best animals turn out to be sterile. Under other circumstances he may prove to have been too pessimistic. Wherever possible, it is important to find out the reasons for any discrepancy.

5. *The degree of heritability and the changes in it during selection.* This implies some prior knowledge of the genetics of the trait involved. Indirect ways of estimating or making first approximations for heritability are usually possible without elaborate experimentation. If no such previous information is available, the kind of data discussed here should be able to provide it.

6. *The extent of non-additive genetic variation.* In addition to additive genetic variation, measured by the degree of heritability in its narrow sense, which is also an index of how effective mass selection can be, there is in most characters genetically determined variation which is non-additive and does not respond to ordinary mass selection. Estimation of this type of variability is not a simple matter since it involves a number of theoretical assumptions and requires large numbers of individuals. However, first approximations can undoubtedly be made in some instances.

7. *Performance.* Knowledge not only of the average performance and variability of each generation or cohort is required, but also of the performance of contemporary controls. Sometimes the control takes the shape of selection in an opposite direction but for a number of reasons unselected controls are to be preferred (see section on control lines in Chapter 8). The extent of operation of natural selection on it should be reported.

8. *Degree and kind of correlated responses.* As already noted, selection for almost any character carries in its wake changes in other traits Linkage or pleiotropy are perhaps the most common causes for such correlated effects. Clearly, the success and efficiency of breeding improvement in one character must be evaluated in terms not only of changes in that trait itself but also in terms of

possible changes in other traits. Since in many tests of selection, correlated responses adversely affecting reproductive characters have been observed, it is particularly important to provide records of the various components of reproduction in both selected and control populations (see section on correlated responses in Chapter 4).

9. *Effects of suspending or reversing selection.* Test populations initiated from the main population at different points in time after selection has been started, in order to determine whether the results of selection are permanent or whether the population tends to regress to its original level if selection is suspended, are necessary to obtain this information. It will be readily seen how much more complicated any experiment is made in terms of design, space and number of test populations by this requirement.

10. *Results from crosses.* Although this is, perhaps, of subsidiary interest, information on what happens when the various selected, suspended or reversed lines are crossed could be very helpful in interpreting the outcome of the rather comprehensive experiment to which all these desiderata refer. Crosses between replicate populations selected in a given direction may provide clues to the selection limits to be expected.

It seems exceedingly unlikely that any experiment with larger animals that has been undertaken to date or that would be practicable in the immediate future could possibly meet all of these requirements. Since experiments so meticulously and thoroughly carried out are not feasible, the interpretation of those that have been made is beset by some difficulties and uncertainties. It becomes virtually impossible to make an absolutely conclusive claim regarding the efficiency of one or another selective procedure applied to useful properties of livestock and poultry. The best that can be done is to make educated guesses and compare roughly the various systems that have been tried; for instance, mass selection for egg number in chickens can be with reasonable assurance shown to be less effective than selection on basis of family testing. Similarly, selection for increased butterfat production within dairy cattle breeds can be asserted to have more effect when it is carried out on the basis of yield and not of coat colour, but the finer shades of discrimination among various selection methods are unfortunately exceedingly difficult to make.

There are still further complications in interpreting results of even the idealised experiment which would meet the criteria so far discussed. The situation with respect to linkage of genes involved in determining the character under selection needs to be known. Is there linkage

disequilibrium? How many effective segregating factors are there? Non-Mendelian effects may be important in determining a given character. It is true that maternal influence can be often estimated and allowed for in interpreting results, but this does not necessarily apply to non-pathogenic infections that may be present, nor to incompatibilities between parent and offspring unless information on this point is available from other sources. Further difficulties may arise out of non-additive genetic variation, the analysis of which itself poses problems. In particular, the scale of measurement which is used to describe the trait under selection may be misleading. All in all, it should be clear that unequivocal demonstrations of the superiority of one or another method of genetic improvement of large animals are unlikely to be obtained, especially if the systems compared differ only a little in their expected results. A system which appears to be the most efficient at one stage may not be the most efficient at a later stage. Consider selection for annual egg record which is based only on early performance. A population in which such selection has not been previously practised will, in the light of several experiments, respond to this method. But a population in which additive genetic variance of the early egg production has been exhausted as a result of selection and, perhaps, inbreeding, will not respond. Indeed, there may also be negative genetic correlations generated between early and later performance so that improvement in the first trait will lead to a decrease in the second, with the result that the total annual egg record will show no change at all.

IV. Selection in Poultry

Among the useful domestic animals there is no doubt that poultry have been the subject of the greatest number of experimental investigations relating to selection. Probably no economic aspect of the chicken's life cycle has been neglected. But, unfortunately, especially in the early experiments, adequate statistical analysis of the procedures used and the results obtained has been lacking. Some selection experiments lasting dozens of generations are on record, yet it is not possible to say from the data published (or for that matter from the data available) whether or not the results completely conform with expectations on the basis of the postulates of population genetics. This is true even of many simply devised experiments in which metric characters of high heritability were utilised.

Perhaps the two experimental flocks that have been subjected to most thorough statistical analysis have been the White Leghorns selected for egg production at the University of California and at

Purdue University. Full details regarding the first of these and a variety of analyses carried out have been reviewed by Lerner (1958) in a schematic form. Should more detailed data be desired, the original papers cited by him should be consulted, as well as the article by Abplanalp (1962). The Purdue data were analysed by Yamada, Bohren, and Crittenden (1958) and in some other aspects by Bohren and McKean (1964). In the briefest possible form the results of both experiments may be summarised in the following fashion.

Selection for increased egg production on the basis of family records appears to follow predictions based on selection differentials used in the early generations of a selection programme. After that, either a decrease or complete cessation of gains is observed in spite of the fact that selection differentials still remain high. The explanation for the change appears to lie in the exhaustion of the kind of genetic variability which is drawn upon by the particular methods of selection used. Relaxation or suspension of selection for egg number does not seem to result in a regression to the unimproved level (although, as is noted later, some drop occurs), but it does seem to be accompanied by correlated responses (even though some selection for the characters thus responding is also involved) in such other traits of reproduction as number of female offspring produced per dam. It is also possible that selection based on part-performance eventually results in a decrease in the remaining part as has been observed in a long-term experiment by Morris (1963). Comparisons of breeding systems, differing for instance, in the use of pullets instead of hens, or in the application of such techniques as multiple shifts of cockerels, indicate that results are in general accordance with those predicted from the general theory. This conclusion is founded partly on the data from the flocks mentioned here and partly results obtained in other populations (see, for instance, Dempster and Lerner, 1957).

Another experiment with poultry also described by Lerner (1958) dealt with mass selection for longer shanks. The original heritability of this trait appears to have been considerably higher than that of egg production and selection was extremely effective until a plateau was reached. Here, however, the plateau seemed to be due less to the exhaustion of genetic variability than to the opposition of natural selection to artificial selection. Apparently the balance of the individual genotypes was destroyed by moving the shank lengths too far from the optimal level for this particular population. As a result, suspension of selection did indeed lead to an immediate regression in the selected trait while reproductive performance improved rapidly in spite of the fact that inbreeding was continued at the same rate as in the selected line.

A more refined test of the adequacy of selection theory in improved flocks has been described by Dickerson (1962). His analysis suggests that when selection has been directed towards multiple objectives for a long time, gains that are expected on the basis of population genetics theory fail to be realised. In every generation of selection offspring from selected parents performed better than unselected controls, but no accumulation of egg production gains was observed.

Dickerson attributes the failure of improvement to continue to negative correlations between components of performance and to genotype-environment interaction which produce at least an operational overdominance. In his opinion modification of the genetic theory for populations that have already been improved is called for.

Basically, the results described in all of these reports are in agreement with the previous conclusions derivable from *Drosophila* experiments (Clayton, Morris and Robertson, 1957; Clayton and Robertson, 1957), that while short-term selection gains are predictable from the simplified theory, long-term ones are not. Furthermore, replicate populations started from a small number of individuals may produce substantially different results as has been noted in the discussion of the founder principle. Still, it should be realised that even short-term prognoses (e.g. twelve generations in the *Drosophila* experiments of Sen and Robertson, 1964) may refer to a period ranging from less than a decade to forty to fifty years depending on the species of domestic animal in question.

To sum up, then, it may be said that the postulates described are, generally speaking, valid for unimproved populations of chickens, and, after the populations reach a certain improved level, they still may hold if the parameters involved have not been changed in the course of selection. The big problem in breeding practice is to discover indications of changes in the rate of selection progress early enough to modify the breeding system.

What has been said so far applies to selection in closed populations. The evidence with respect to other breeding systems in poultry is much less complete. Although a large number of breeders have put into effect selection for combining ability, which, if operational criteria are a guide, must have been successful, the published experimental evidence is rather scanty. It is thus not yet possible to check the exact assumptions which are made in the theory of breeding for combining ability.

The last point that need be given brief mention in this section is the effect of relaxation or suspension of selection. The theoretical aspects of the problem were considered by Robertson (1956) who introduced

the concept of homoeostatic strength, a parameter measuring the degree to which the mean of a selected population returns towards the original equilibrium. Experimental evidence in chickens and a review of related literature is given by Nordskog and Giesbrecht (1964). Apparently, for rate of egg production, a decline of the order of 0·75–2·25%, exclusive of inbreeding effects, may be expected per generation after suspension of selection. This corresponds to a loss of three to nine eggs per bird per year. With respect to egg weight, which is normally maintained by artificial selection at a level higher than that of the point of maximum reproductive fitness (Lerner, 1951), the decline may be even more severe. Indeed, one of the important problems in poultry breeding practice is how to avoid having to sacrifice some selection pressure for egg number in order to maintain egg size. The moral is that selection for many traits, even after a plateau in performance has been reached, must be continued lest regression occurs. The thought from *Alice Through the Looking Glass* of running fast in order to stay in the same place involuntarily comes to mind.

V. Evidence from Larger Animals

For obvious reasons, the extensive material available to laboratory geneticists, to plant breeders and even to workers with poultry, has not been available to geneticists interested in the larger animals. The number of controlled selection experiments on livestock conducted on a sufficiently large scale to permit accurate comparison of the results obtained and the results expected is very small. As a rule, other types of data must then be relied upon to demonstrate that there are no special forms of inheritance peculiar to livestock and that the main tenets of genetic theory derived from other organisms are equally applicable to cattle, pigs and sheep.

Most selection experiments with these animals suffer from a variety of complications (lack of controls, concurrent close inbreeding, small numbers, environmental changes and others). It is difficult to find convincing examples of selection results for dairy cattle, in spite of the long-continued programmes of research on the effect of selection of superior sires, of progeny testing, and of artificial insemination.

For beef cattle, Brinks, Clark and Kieffer (1965) have recently reported on a study of selection in a closed herd of Herefords in which thirty-three sires were used over a period of twenty-five years to sire over 2000 weaned offspring. Three of their conclusions having a bearing on the present discussion may be quoted:

1. "Estimates of genetic changes, calculated by subtracting the environmental trend from the phenotypic trend, indicate that substantial genetic progress was obtained for birth weight, gain from birth to weaning, weaning weight, and weaning score. Estimates of total genetic response from 1934 through 1959 were 9·7 lb in birth weight, 21 lb in gain from birth to weaning, 30 lb in weaning weight and 6·5% in weaning score."

2. "Comparisons of expected and estimated genetic response from 1943 through 1959 indicate that slightly more response than expected was obtained in birth weight (106%) and weaning score (116%), and considerably more than expected was obtained in gain from birth to weaning (139%) and weaning weight (130%). Adjustment for detrimental effects of inbreeding were not included in these values. If adjustments for the effects of inbreeding had been made, estimates of considerably more progress than expected would have been obtained in these traits."

3. "Comparisons of expected genetic response and actual phenotypic response for postweaning traits from 1943 through 1959 indicate that, in general, the actual response was as great as or greater than expected. Although environment is a factor in these trends, there apparently has been some genetic response, and the data do not suggest that this response is less than expected."

For swine, Dettmers, Rempel and Comstock (1965) have reported a successful eleven-year programme of developing in Minnesota a strain of miniature pigs for medical research. Body weight at 140 days was reduced by at least 29%, the latest average (for 99 pigs farrowed in 1961) being 38·6 lb. Here again, there were neither controls nor selection in opposite directions. Another experiment carried out in Illinois by Craig, Norton and Terrill (1956) did include two-way selection, for large (ten generations) and for small (eight generations) size. The two lines showed increasing divergence which rose to 50 lb at 180 days of age in the last comparison made. The results were consistent with a heritability of 0·16–0·17 for the trait, falling (contrary to the Minnesota experiment) somewhat short of the usual heritability estimates for body weight.

For sheep, a successful outcome of two-way selection (plus a control line) for multiple births in New Zealand Romneys was reported by Wallace (1958). Although there are statistical complications in interpreting his results, Table 3.1 shows that the lambing percentages of the high line, the control and the low line showed increasing divergences. Earlier heritability values for this character were so low as to suggest that selection in it would be futile. They seem to have been underestimates for this population, as well as for Australian Merinos in which

Turner *et al.* (1962) were also able to increase the percentage of multiple births.

Finally, interim results of selection in Scottish Blackface sheep (A. F. Purser, personal communication) may be given to illustrate a test of genetic theory on the basis of a more precisely designed experiment than is usually possible with larger animals. Four selection and two control lines of about 250 ewes each were started from the same base stock. Two were devoted to changing cannon bone length (as measured at 6 weeks of age) in opposite directions. In two other lines, plus and minus selection pressures for the amount of medullation

TABLE 3.1

Lambing % difference in a two-way selection experiment (from Wallace, 1958)

	Lambs born/ewes lambing			
	High line — control		High line — low line	
Age	First 5 years of experiment	Last 5 years of experiment	First 5 years of experiment	Last 5 years of experiment
2	6	9	7	10
3	7	11	8	12
4	8	21	13	23
5	14	18	18	29
6	31	42	39	42

in samples of mid-side wool at 6 weeks of age were applied. Fortunately, both characters showed, as previous work had forecast, sufficiently high heritability to permit effective selection on each individual's own performance. Heritability for medullation was 0·55 and for cannon-bone length 0·59. With this information and a knowledge of the measurements of the animals chosen for breeding, it is possible to estimate the progress that should be made if no attention is paid to any other character (as is the case here). The comparison of observed and expected gains is shown in Fig. 3.1, which shows the divergence between the pairs of complementary lines. There is no reason to suppose that the results obtained deviate markedly from those expected. There may be a hint that realised progress is tending to fall somewhat behind expectation, but it is too soon to be sure whether this is, indeed, so. If it is, there will be no shortage of possible reasons.

Other types of evidence of the correspondence between genetic theory and the actual working of inheritance in livestock come from pedigree analysis, from twin data, and from the results of inbreeding.

The first of these deals with Mendelian traits These are superficially simple characters such as blood groups, which can be clearly followed from one generation to another Their presence is easily recognised and they are demonstrably transmitted according to the rules which Mendel discovered Although various qualifications are usually attached, the rules account for most of the observed variation and permit sound predictions to be made Because these are now generally acceptable,

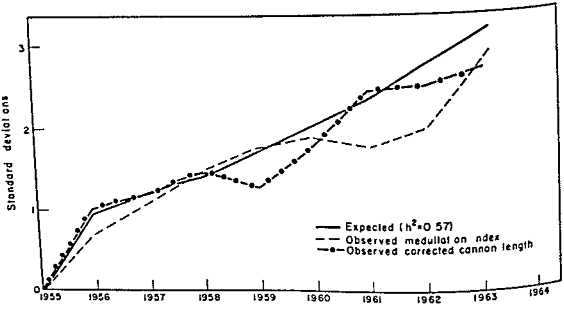


Fig 3 1 Observed and expected divergence in sheep selected in opposite directions for cannon length and amount of medullation (from A F Purser, unpublished)

the use of blood groups in clearing up ambiguities of parentage has become possible Of recent years there has been a notable growth in the number of biochemical variants known to behave in Mendelian fashion so that the prospect of being able to identify linkage groups is drawing closer Apart from the numerous blood groups found in cattle, pigs and sheep there are recognisable varieties of protein in blood serum and milk (discussed in Chapter 9) the familiar colour patterns, and many other simply inherited characters (Hutt 1964) Besides such textbook examples there are numerous lethals sublethals and deleterious genes, most of which unlike those responsible for dwarfism in beef cattle, are not being fully investigated Many of them would no doubt be found to behave in a simple Mendelian fashion

The use of twins in genetic research is based on the fact that the closer the genetic relation between individuals, the greater is the phenotypic resemblance between them There are two kinds of twins in cattle

identical (monozygotic) and fraternal (dizygotic). As in man, the members of an identical pair are exactly alike in all traits, such as blood groups, that are wholly determined by heredity. By contrast, fraternal twins, with some exceptions caused by common foetal circulation, are no more alike in such traits than full brothers or sisters. Comparisons of resemblance within pairs of the two kinds of twins can be extended by investigating pairs of less related individuals, such as half-sibs or second cousins, or completely unrelated animals. If all kinds of pairs are born at the same time and studied on the same farm,

TABLE 3.2

Intra-pair correlations in Ayrshire cows milked for at least 100 days
(H. P. Donald, unpublished)

Kind of pair	Monozygotic twins		Dizygotic twins		Half sisters		Unrelated pairs	
Lactation	1	2	1	2	1	2	1	2
Days in milk	0.57	0.40	0.48	0.46	0.33	0.63	0.20	−0.38
305 day milk yield	0.85	0.65	0.59	0.35	0.34	0.53	0.25	−0.13
70 day milk yield	0.73	0.49	0.48	0.29	0.11	0.49	0.15	0·13
Butterfat %	0.96	0.91	0.57	0.69	0.16	0.13	0.18	0.07
S.N.F. %	0.90	0.81	0.66	0.51	0.37	0.56	0·14	0.22
Casein %	0.91	0.84	0.63	0.48	0.21	0.35	0.11	0.34
Non-casein protein %	0.87	0.57	0.52	0.55	0.57	0.24	0.07	0.24
Lactose %	0.79	0.51	0.82	0.50	0.26	0.60	0.28	0.25
Body weight at 18 months	0.90	0.90	0.53	0.54	0.55	0.52	0.33	0.32
Number of pairs	26	21	28	22	28	21	36	26
Value of correlation at 5% level of significance	0.38	0.43	0.37	0.42	0.37	0.43	0.33	0.38
Average correlation	0.83	0.68	0.59	0.49	0.32	0.45	0.19	0.12

they can all be expected to show that an animal resembles its own specific mate to some degree simply because of the common environment that has been imposed. Beyond this, however, it would be expected on theoretical grounds that the more closely related the two members of a pair, the more alike they will be. This in fact is just what has been found, as Table 3.2 shows.

In it are entered the intra pair correlations (as a measure of resemblance of pair mates) for four categories of pairs ranging from identical through fraternal and half sister to unrelated pairs. All were reared in one herd on the same farm from the age of about seven days. With such limited numbers of pairs the correlations have large sampling errors, but as the average values at the bottom of the table show, the diminishing similarity in performance as the relationship weakens is quite obvious.

Since there is some resemblance in unrelated pairs, they may be providing a measure of the extent to which the two environments of a pair are correlated because they have been reared and milked together and thus shared, at least in part, the same ups and downs of life.

How steeply the gradient of similarity rises towards the identical pairs depends on how heritable the characters studied are, on the importance of prenatal environment (which is the same for twins but not for non twins), and on whether or not environmental correlations are the same for all kinds of pairs. About this last point not much is known, but it is an absorbing question. Each animal is an important part of the environment of the other member of the pair and yet its nature is largely determined by heredity. Therefore to some extent, the environment of an animal is determined by its own genotype. The same sort of complexity could arise with infections or induced behaviour patterns. For this and other reasons, it is not to be supposed that 'on the same farm' means that all animals have the same environments. Those born at same season, and of similar mothers and penned together will have much more highly correlated environments than those which share no more than the soil, climate, vegetation and general management. For more details on cattle twins, Donald (1959) and Johansson (1959) may be consulted.

Resemblance between cattle twins is only a special case of resemblance between litter mates. The mass of information about resemblance between relatives and most heritability estimates come, however, from the comparison of groups of half sisters by the same sire. When heritabilities are very low, half sibs resemble each other hardly more than unrelated animals, and when they are high, half sibs show a much closer similarity than unrelated animals (Lush, 1945, Lerner, 1958, Falconer, 1960).

The remaining fruitful source of information on the mechanism of inheritance in farm animals comes from inbreeding investigations. Although the unfortunate consequences that follow the mating of close relatives were discovered a long time ago, the practice of inbreeding

during the formation of some breeds, especially the Shorthorn, gave rise to the notion that in the hands of a constructive breeder, inbreeding had at least a therapeutic value due to cleansing the stock of bad characters while at best it concentrated good characters. This view persists widely to this day. With the development of the theory of inbreeding by Wright (1921), however, a quantitative approach to inbreeding data became possible.

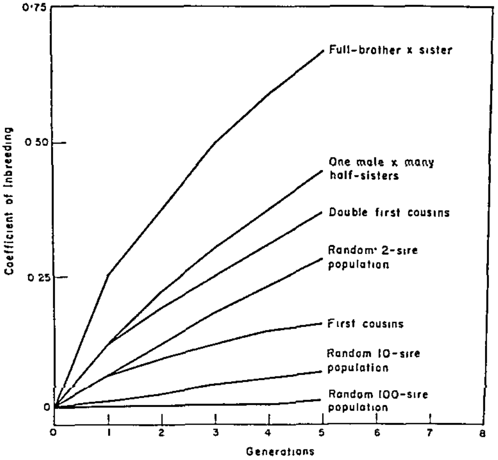


Fig. 3.2. Increase in homozygosity under inbreeding (derived by Lerner, 1958, from Wright's classical study, 1921, and reproduced with permission of the publisher).

Figure 3.2 summarises the expected genetic results of different degrees of inbreeding. They are measured in terms of a coefficient, F, lying between 0 and 1. Technically, F expresses the probability that the two alleles at a locus which enter a zygote are derived from an ancestral allele common to both; or, alternatively, it can be thought of as the proportionate decline in the average number of heterozygous loci carried by a randomly chosen individual within a given population. To use an extreme but common example, a one-sire herd that is self-contained must in due course use a son of that sire on female descendants of that sire. Each mating then traces back to one instead of two or more

sires. Such a mating is shown in Fig. 3.2 as one male × many half-sisters. This is not the strongest type of inbreeding but it brings about a loss of almost half the available genetic variation if kept up for six generations. When breeders speak of inbreeding or line breeding they rarely mean a mating scheme as intense or as long-continued as this. Because heterozygotes are more vigorous, natural selection may operate in their favour so that the computed degree of homozygosity is probably often an overestimate of the attained level.

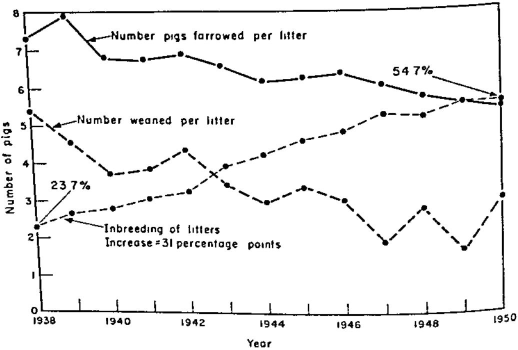


Fig. 3.3. Decline of performance in reproduction as a function of inbreeding for Poland China one sire herds (from Craft, 1953)

What Fig. 3.2 does not show is that increasing the proportion of homozygous loci is accompanied by a loss not only of genetic variability (which may be desired) but also of vigour, viability, fertility and milk production (which is usually not desired). Many experiments (for example, Brinks, Clark and Kieffer, 1965, for beef cattle) have confirmed that what is called inbreeding degeneration in livestock is roughly proportional to the amount of inbreeding. It appears not to matter much which of the lines in Fig. 3.2 is followed. What matters is the size of the coefficient. Any breeder therefore who inbreeds, can be sure (save for accidents of sampling) of some deterioration. In well-investigated subjects, such as litter size in pigs, he can be advised of the likely loss he will incur by his inbreeding. An example of decline under

inbreeding is shown in Fig. 3.3. Other instances and a technical discussion of inbreeding degeneration are to be found in Lerner (1954).

A breeding programme based on a very few highly selected males clearly leads very quickly to inbreeding. It then becomes a question of compromising somewhere between the advantages of rigorous selection and the disadvantages of inbreeding. Looked at in a slightly different way, inbreeding and crossbreeding are deviations on either side of outbreeding which are likely to develop as selection tightens.

There is no serious alternative to genetic theory as a basis for practical animal breeding. Livestock have been the stimulus and the material for the development of the large part of it known as population genetics. In the preceding paragraphs, an attempt has been made to give a rough idea of the sort of evidence available but it is not to be supposed that the various categories discussed have any basic genetic independence of each other, or that they hint at more than a small fraction of the known facts, many of which are drawn from animals and plants of limited agricultural importance. The risk of labouring this point is taken because there is sometimes a temptation for practical breeders and officials to suppose that what they do not know about breeding livestock is not knowledge, or that because the particular breeds they are interested in have not been subject to trial and experiment, nothing is known about their behaviour.

In general, it is easy enough to fault current theory and it is often done. But the theory will improve with use. Although no amount of algebra or genetics will remove the influence of chance, forecast economic changes, or insure against political acts, there is no going back to the mystique of pedigree breeding which had these same deficiencies.

Since there is no immediate prospect of reducing generation intervals substantially, fears of disastrous errors due to applying breeding theory to practical situations have little foundation. Rates of change in the genetic constitution of animal populations are so slow that it is difficult to establish whether or not a change is taking place in any direction. The only reason for trying to apply genetic principles is to gain a better measure of control and thereby a better response to selective breeding. None of the principles, however, will secure progress if they are nullified by lack of consistent objectives or by over-complex specifications. Knowledge of genetic correlations is admittedly fragmentary and it is often open to anyone to assume favourable or unfavourable consequences of a selection policy as he wishes. Whether or not to risk an unfavourable outcome is largely a matter of temperament. But most progress is made by the risk-takers.

On the evidence, there can be no reasonable doubt that the main assertions of population genetics are correct in essentials and are a sound basis for industrial development. Although there is much to be done by geneticists in strengthening and developing the structure, its grand design is unlikely to change much.

Where there is controversy between breeders and geneticists, it is mostly about aims, less about methods and not at all about theory. Aims are for breeders, large or small, to fix but if they insist on including in their aims not only characters of low economic value, but also methods such as eye judgment and small breeding groups of low efficiency, they must expect to have to defend themselves against criticism from other interested groups. They must expect also to have to meet competition from livestock bred with different aims and methods.

CHAPTER 4

IMPROVEMENT METHODS

A full discussion of breeding methods now in use falls outside the scope of this book. There are many texts which cover this subject. Descriptions written by different authorities and dealing with beef cattle, dairy cattle, swine, sheep and goats, horses, and poultry may be found in the volume edited by Cole (1962). The chapter on livestock breeding in Byerly (1964) also gives a summary of the generally accepted practices in the United States.

There is a great deal of variation both among the methods employed for the different species in a given country and among countries for the same species. In part, this variation is traceable to the dissimilarities in the biological properties of each kind of animal, and, in part, to the differences in the level of technology achieved. Not surprisingly, the most complex and thorough procedures are found in poultry, and the least advanced methods are used (with some exceptions in countries where they are of great economic significance) in sheep. In between, lie swine, dairy and beef cattle, the improvement of which depends on techniques, sometimes as organised as the elaborate Danish performance testing of pigs (Lush, 1936) or progeny testing of bulls used in artificial insemination (Johansson, 1961), and sometimes harking back a century or more to the show-ring. The upper section of Table 5.2, which gives a broad survey of the situation in the different species of livestock, may be consulted for a comparison of the usual breeding methods applied to them.

This chapter deals mainly with certain features of the techniques and problems encountered in animal improvement which are significant in the context of this book. In essence, breeding procedures must rest on four points:

1. there should be material on which the breeder can exercise his powers of selection, i.e. genetic variability is a prerequisite to genetic improvement;
2. the methods available to the breeder (primarily selection and control of the mating plan) must be based on adequate information, including performance testing and evaluation;
3. decisions as to whether the breeder is concerned with short or long-range results must be taken;
4. the breeding scheme must be chosen on the basis of minimum costs per unit gain.

The following sections deal with some of the issues arising from these principles.

I. Performance Testing

Probably the most important single events in the history of performance testing were the invention of the trapnest for recording egg production, the introduction of the Babcock test for assaying the percentage of butterfat in milk, and the development of probes and ultrasonic devices for measuring the amount of backfat in pigs. All of these techniques are applicable not only in testing stations but are also suitable for on-the-farm tests. The merits of these two forms of recording depend on the purpose of testing and on the animal concerned. In poultry, each breeder usually depends on his own recording for selection, sometimes entirely on his own farm and sometimes (especially for testing hybrid or cross-bred combinations) on private egg-production farms in different locations. For public comparisons with other breeders (which basically implies advertising purposes), central egg-laying tests are used. In dairy cattle, with the increasing use of progeny testing of bulls for artificial insemination, on-the-farm recording is widely employed. Indeed, the American Dairy Herd Improvement Association considers farm testing as reliable as central testing (which, of course, can be carried out in a standardised environment). Furthermore, the costs of centralised testing of larger animals in sufficient numbers (examined for European conditions by Johansson, 1960) seem to be prohibitive.

The Danish progeny testing scheme for swine, however, is based on central testing stations, as are feed-lot tests of cattle in several parts of the United States. Tests on sheep have been conducted both on the individual farms (e g. in Wisconsin, Ohio and England), and in central stations (e g in Texas and Utah).

The superiority of one or the other method hinges mainly on three issues. cost, heritability and genotype-environment interaction. The

relevance of the first of these items is self-evident. As for the second, traits with high heritability, such as growth rate on a given diet, fleece weight and egg size are usually not much affected by location, and, therefore, can be accurately evaluated on the breeders' own premises. Characters of lower heritability, such as egg production, may be more informatively tested if there is a variety of conditions. This can apply only to inter-line or inter-strain selection and not to selection within populations except for progeny tests carried out on the scale made possible by artificial insemination.

With respect to genotype-environment interaction, that is to say, a differential response of a genotype in different environments, objections have been raised to relying only on testing stations on the grounds that the genetic value of locally adapted types is underestimated when all recording is done under one system of management and one set of environmental conditions. Evidence that some breeds or strains are superior under some conditions and inferior under others is not difficult to find, especially, if the conditions and the genotypes are, respectively, widely disparate. Statistical evidence of interactions from comparisons with narrower limits can also be found (e.g. Dickerson, 1962b), but the amount of variation attributable to these interactions is relatively small. Furthermore, to identify the sources of weakness and strength of particular strains is proving very difficult and quite impossible to predict in advance. It seems likely that genotype-environment interactions will be found to be numerous, sometimes exaggerating, sometimes counteracting each other, and influencing mainly those characters which are most subject to inbreeding depression. These are traits such as fertility and mortality and other components of fitness which have very low heritabilities and show very large amounts of apparently nonheritable variation. It might be found, in due course, that most of the genotype-environment interactions occur at the individual rather than at the strain or breed level. It also could happen that genotype-environment interactions are self-cancelling in the sense that sometimes they are favourable and sometimes unfavourable during the course of the history of a single individual. Young animals may be reacting to infections of one sort or another with a partially or unequally developed apparatus of immunological tolerance or protection. Later on, they may be choosing their own environments in such a way as to run more risks than others of a similar kind and with similar opportunities. Accident proneness could be a significant characteristic of animals.

An allied problem in testing arises from interactions between individuals within a population. Every animal in a flock, herd or testing

station is part of the environment of other individuals (see the general reviews of this issue as it occurs in natural populations in Andrewartha and Birch, 1954, and Wynne-Edwards, 1962, and for domestic animals, Hafez and Lindsay, 1965). This is self-evident, but nowhere more so than in the behaviour of identical twins, both human and bovine. Moreover, some of the environment of one such twin which the other provides is to a degree genetically determined. Consequently, a part of the environment of a twin is conditioned by its own genotype. The same will apply to any pair of animals but with lessening force as relationship becomes more remote.

Other well known examples come from the behaviour pattern of many animals from man downwards known as the peck order. Fitness in a particular environment must include the correct and successful responses to social and actual stimuli offered by other members of a group. As a result, performance is connected with the position of an animal in the intra-group social order (see McBride, 1964, for chickens, and McBride, James, and Wyeth, 1965, for pigs). This problem also exists on the strain level. The question may be asked whether different lines of chickens under test should be raised separately, thus introducing differences between their pen environments, or together, thus injecting social rank-performance genotype interactions, which would not be present under the actual conditions of production.

In general, whenever changes in the environment of domestic animals occur, it could happen that temperament and behaviour would be highly important factors in finding adapted strains or breeds. Individually fed pigs have a different order of merit from group fed pigs; indoor sheep will differ from outdoor sheep; intensively kept poultry from those maintained under extensive conditions. Genotype-environment interactions of this sort may be commoner than is realised. Domestication itself provides the outstanding evidence of the way they can be turned to good use.

The main issue that faces the breeder is to find a compromise between accuracy, on the one hand, and costs of testing, on the other. It is evident that a single lactation record will not evaluate a cow's genotype for milk yield exactly, but at the same time, a full 305-day record for each lactation is not necessary. It is equally clear that trapnesting a chicken seven days a week is a wasteful procedure when doing it only three days a week provides sufficient accuracy in selection. The particular compromises adapted for the different traits of the various species are, of course, a technical matter. They are considered in the general references to breeding methods already cited (see also Chapter 5).

II. Progeny and Sib Tests

The most common method of choosing the parents of the next generation from a population is mass or individual selection. Aids for evaluating the genotype, and, hence, the breeding worth of individuals are provided by progeny and sib tests. When a character under selection has very high heritability, information on the performance of relatives, in addition to that on the individual considered as a potential parent, will augment the accuracy of the estimate of its genotype only a little. Important exceptions are sex-limited traits, such as milk or egg production, and characters (e.g. carcass quality or performance as a steer in a feed lot) which cannot be measured on a breeding animal. In contrast, when heritability is low, the phenotype of an individual gives only a very limited clue to its genotypic merit, and data on its relatives (usually progeny or sibs) must be relied upon in selection.

The question of whether progeny and sib tests are to be employed and, if so, to what degree, is, therefore, an operational one. It was first thoroughly explored by Dickerson and Hazel (1944), who viewed the problem in the light of gains to be expected from different selection methods, including those relying on individual records, pedigrees, sib tests and progeny testing. In addition to heritability, the interval between generations (i.e. the average age of the parents when the offspring are produced) and the reproductive rate need be known for a valid comparison of the different selection methods. The use of such comparisons for poultry has been described by Dempster and Lerner (1947). But neither they nor Dickerson and Hazel have considered another feature of operational significance, namely, the financial aspects of carrying out the different forms of testing. Yet another factor is the decrease in the potential limits of improvements which is caused by the use of family records (see the section on costs of change in this chapter).

In their original study, Dickerson and Hazel concluded that regular progeny testing is unlikely to increase, and may actually reduce, rate of genetic gain, "unless (1) the progeny-test information becomes available early in the test animal's lifetime, (2) the reproductive rate is low, and (3) the basis for making early selections is relatively inaccurate." However, they also pointed out that extension of artificial insemination to large populations would increase the advantages of progeny testing for sheep and cattle. This is what happened in the selection of dairy cattle sires, wherever organisation of artificial breeding has become extensive, as in Britain where at the time that the Dickerson and Hazel article was published, the number of artificially inseminated

cows stood at about 4000 a year, whereas twenty years later, the comparable figure was over 2 million.

Selection under these circumstances must then rely more and more on evaluation of genetic merit of sires on the basis of progeny tests. Some questions of crucial operational significance immediately present themselves. Thus, Henderson (1964) addressed himself to the method of selecting bulls for testing and concluded that only a partial solution to the problem is possible. The obvious place to find promising young sires is among the sons of sires already proven to be of outstanding merit, out of dams who are themselves by outstanding sires and of high performance. Yet, even this method of selection offers no certainty that the young sires will be good, since the practical upper limit to the correlation between the estimates of genetic merit on basis of ancestry and the actual genotypic worth of young sires is only about 0·67. This means that, at most, $(0{\cdot}67)^2$, or 45% of the genetic variation among untested sons can be accounted for by the fullest information on the parents.

How to determine the number of daughters needed from sires under test was examined in a comprehensive theoretical fashion by Skjervold (1963) and Skjervold and Langholz (1964, 1964a), who obtained general expressions for optimal breeding structure of populations reproduced by artificial insemination, taking into account testing capacity, selection intensity, degree of heritability, maternal effects, and inbreeding depression. More specifically, Van Vleck (1964), who made a study of bull-testing schemes for the artificial insemination centre at Cornell, found that the maximum genetic improvement will be obtained when a large number of young sires are judged by twenty to fifty daughters each. It also turned out that the schemes producing the highest genetic gains were the most profitable ones.

It will be readily appreciated that in a changing situation specific answers to questions of this type can have no finality. A running re-evaluation, not only of the parameters to be used in solving the mathematical equations, but also of the formulae themselves is desirable. It seems indisputable that applied research of this type will be needed to ensure that the money allocated for improvement is spent to the best advantage. When dealing with progeny testing on the scale now developing in cattle, playing by ear will no longer do. This is a lesson that future decision makers for other kinds of breeding enterprises should remember.

III. Selection Indexes

When several criteria are employed in the estimation of genetic merit, they may be combined into a single figure known as the selection index.

The use of indexes of various kinds is not a new practice. Simultaneous selection for egg number and viability in chickens has been based on family average egg production per original bird housed, essentially, an index. However, the genetic theory which made it possible to assign proper weights to each criterion so as to maximise genetic gains was worked out considerably later (Smith, 1936; Hazel, 1943). Various aspects of index selection, including methods of construction, are discussed by Hazel and Lush (1942), Lerner (1950), Dickerson (1955), and Kempthorne (1957). More recently, the relative efficiencies of index selection and of other methods were examined by Young (1961) and by Finney (1962).

TABLE 4.1

Values of the parameters needed in computing a selection index for bacon pigs (adapted from compilation of Smith and Ross, 1965)

Traits	1	2	3	4	5	6	7	8	9
1. Daily gain	*·42*	·73	−·17	·07	−·07	·13	−·13	·10	−·03
2. Feed efficiency	·76	*·48*	·05	·04	−·19	·17	·16	·17	·16
3. Dressing-out %	−·19	−·01	*·32*	−·19	·19	−·06	·29	·22	·15
4. Carcass length	·14	·08	−·40	*·62*	−·22	·37	−·14	−·19	−·05
5. Backfat thickness	−·15	−·21	·28	−·30	*·54*	−·34	·13	·12	−·13
6. Carcass conformation	·28	·30	0	·46	−·52	*·28*	−·17	·36	·24
7. Belly thickness	−·03	−·10	·25	−·17	·22	−·13	*·38*	·07	−·07
8. Ham score	·14	·24	·34	−·23	−·26	·37	·19	*·36*	·27
9. Eye muscle area	−·11	·34	·36	−·08	−·28	·35	−·16	·44	*·42*

Heritabilities are shown on the diagonal; phenotypic correlations appear above diagonal; genetic correlations below. Note that feed efficiency here refers to weight gained per pound of food consumed.

The biological information necessary to construct an index includes the heritability of the relevant traits (Spector, 1956, has a compilation of estimates for domestic animals), and the genetic and phenotypic correlations among them (Tables 4.1 and 4.2 give examples for pigs and cattle, respectively). In addition, the economic value of each character has to be known. Usually, it is impracticable, except in very large establishments, for an individual breeder to obtain the appropriate heritability and correlation figures. For many unimproved populations, however, they appear to fall within similar ranges of magnitude and, therefore, published values may be used. In highly improved populations, these figures may no longer be applicable: successful selection may

have reduced heritabilities and greatly changed correlations between traits (see the section on correlated responses). Hence, a breeder using a selection index needs to verify periodically whether the figures used in its construction are still correct.

TABLE 4.2

Estimates of correlations between milk production and other characters of dairy cows (based on compilations by Farthing and Legates, 1957, and Johansson, 1961a)

Character		Correlation Phenotypic	Genetic
Body size		0·31	0·26
Growth rate		+	?
Muscle development		—	—
Services per conception		0	?
Incidence of oviduct cysts		+	?
% butterfat	Jersey	−0·36	−0·50
	Guernsey	−0·32	−0·57
	Guernsey	−0·34	−0·77
	Holstein	−0·22	−0·38
	Holstein	−0·25	−0·21
	Holstein	−0·10	−0·52
	Ayrshire	−0·14	−0·20

The problem of weighting for economic worth is even more difficult. For some characters economic values must be mere guesses, while for others they may fluctuate widely from year to year. The results of selection using a given index may not be available for years and by then, the economic values may be quite different from those used in its construction. Thus before the first World War, an index used in the selection of Yorkshire pigs would have carried a positive economic weight for thickness of backfat; after the war, the sign of the economic value for this character would have become negative.

An even more complex problem is how to decide on the economic value whenever the objectives include both traits of importance to the purchaser of stock and to the breeder. As an example, the grower of broiler chicks is interested in growth rate and carcass quality. He has no concern with fertility and hatchability. Yet the breeder's financial success depends as much on the reproductive capacity of his stock as on

its average genotype for broiler qualities. In one case, the criterion is based on the value the grower will obtain if he purchases stock from the breeder; in the other, the value depends on the money the breeder can make by selling his stock to the growers. For poultry at least, the argument that good fertility is important to growers because it reduces their costs is not very strong, since the initial outlay per chick forms a rather small part of the total cost of raising broilers.

Despite the various complications, indexes have been constructed for all classes of livestock, and, within each, for a variety of purposes. In poultry, selection indexes have been extensively used in commercial practice (Dickerson, 1962). With many traits included in an index (and some characters might appear in an index several times in the shape of individual records and different kinds of family averages) and populations containing thousands of individuals, for each one of which an index value must be calculated, index selection is an operation for a computer, and a costly one. Hence, it is important that the gains in increased efficiency expected from index selection be compared with the costs of using this method before it is adopted.

There are four kinds of purposes to which selection indexes can be put:

1. In selection for a single trait, an index incorporating information on the individual and on its various relatives, ancestors, collaterals or descendants, increases the accuracy of estimation of the animal's genetic merit, especially for traits of low heritability. Because improvement in only one character is sought, the task of estimating correlations between traits and of assigning relative economic merit is avoided. However, it is unrealistic to suppose that selection of this type can have much practical significance. Reproductive capacity, health, efficiency of feed utilisation and adaptation to environment, all must enter in one way or another into selection for any economically important objective. In fact, every economic property is no doubt a compound of many traits. Basing selection on some combination of these does not make it a "single character".

2. *Selection may be directed primarily to one trait, but the index* may incorporate information on other traits as an aid in identifying genetic merit. If the trait selected for has low heritability but has genetic correlations of appreciable degree with other characters, the latter may be appropriately included in the index, with zero economic values assigned to them.

3. A similar situation prevails when selection directed towards one trait produces undesirable shifts in other traits genetically correlated with it. Indexes in which zero economic weights are

assigned to them may be designed so as to leave their means relatively unchanged, while the character selected for is improved.

4. The most important use for selection indexes is in breeding populations where multiple objectives are pursued. Whether they are expressed in terms of individual characters such as growth rate, conformation or carcass quality, or of a compound such as monetary value of a litter, the index will have several items in it and the same character may appear in more than one of them. Occasionally, superficial paradoxes in construction of indexes of this kind are encountered. For example, in Hazel's (1943) original study of index selection in pigs, he found that carcass score contributed to the total monetary value. But the phenotypic correlation of this character with the economically more important 180-day body weight was higher than the genetic correlation. In these circumstances, because of certain biometrical properties, an index in which market score is given a negative weighting is found to be more efficient than one in which it is ignored.

When selection for several traits is practised, three methods of procedure are available: (a) each trait can be selected for separately and simultaneously (selection by independent culling levels), (b) one trait at a time could be selected in succession (tandem selection), and (c) selection on all traits could be carried out simultaneously by using a selection index. It has been shown by Hazel and Lush (1942), and by Young (1961) that the third method is theoretically never inferior to selection by independent culling levels, which in turn is as at least as efficient as tandem selection. There is no reason to believe that the theory is faulty, though only limited experimental support for it (e g. Abplanalp, Asmundson, and Lerner, 1960) is available. It must, however, be realised that there are some problems in selection that no index can solve. Thus, if a high negative genetic correlation exists between two traits, because the same genes enter into their determination, it is impossible to improve one without the other suffering deterioration. Selection for short shanks and high body weight of chickens would probably be self-defeating as a result of such a situation (Lerner, Asmundson, and Cruden, 1947). In a similar case, Merritt and Slen (1963) appear to have broken up genetic correlations between body weights at different ages (suggesting that some of the correlation was due to linkage) by selection. All in all, though there are difficulties in striving for multiple goals, the invention of the selection index has done much to minimise them. It is true that in the past breeders have made changes in their flocks and herds without the help of this device. But it is also true that improvement was neither fast nor certain. If there is to

be a speeding-up of the rate of progress, more use of statistical aids such as the selection index will be needed.

IV. Heterosis and Crossbreeding

Perhaps the greatest change in animal breeding procedures of recent decades has been the increase in systematic crossbreeding and crossing between lines and strains as an alternative to purebreeding. There are many variants of these procedures. Some may involve selection for combining ability such as the reciprocal recurrent selection illustrated

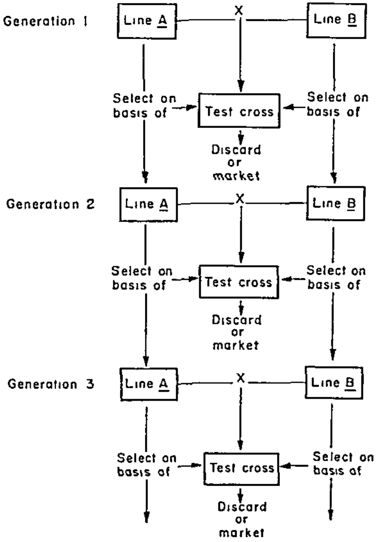


Fig. 4.1. Reciprocal recurrent selection.

in Fig. 4.1. This method may be utilised within a breed as well as between breeds. Other techniques are based on systematic crossing of two or more breeds. Several schemes used in pigs are shown in Fig. 4.2. Still other variants are described by Lerner (1958).

Both the extent and the purposes of crossbreeding vary between species and countries, but livestock production has become heavily dependent on it (see section on stratification in Chapter 6) In the United States, nearly all broilers are of crossbred origin, 80% of the swine come from breed or line crosses, crossbreeding similarly dominates sheep production The main exception lies in range bred beef cattle, though some crossing is beginning to take place also in this class Dairy cattle form a special category crossbreeding here is founded on the use of beef bulls in order to improve the meat quality of offspring not intended for milking From the figures published by the Milk Marketing Board, it appears that in England and Wales in 1963, over 40% of all artificial inseminations of dairy cattle were made with semen from beef bulls

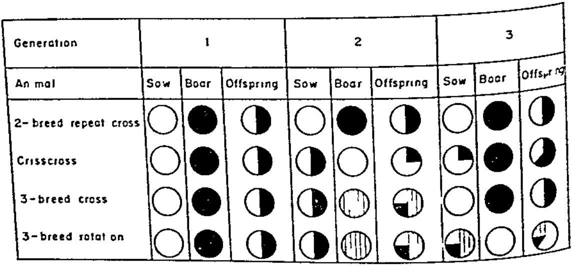


Fig 4 2 Examples of crossbreeding schemes for pigs (adapted from Durham in Cole, 196?).

Resort to crossbreeding may also be had for other reasons Hybrid vigour or heterosis is one of them rectification of some defect of a pure bred is another Some breeders may merely wish to introduce new genetic variability into an existing gene pool But generally speaking crossbreds are popular because they have the right kind of performance The advantages so obtained justify recommendations to livestock producers to increase the extent of crossing (see for instance, Sharman, 1963 and 1965 on sheep and pigs, respectively)

Refinement of crossbreeding techniques has been carried farthest for chickens Selection may be practised within lines or breeds for general combining ability with any other strain or breed or for combining ability with another specific parent (Merritt and Gowe, 1960, discuss this issue with regard to broilers) Mass creation of inbred lines for

eventual crossing (often within a breed) is a widespread tool used by breeders of laying stock.

In larger animals, crossbreeding sometimes replaces selection rather than supplements it. As might be expected, pigs, which have a relatively rapid rate of reproduction and exploit a narrow range of nutritional conditions, lend themselves to poultry methods more easily than cattle. Much effort has been put into developing inbred lines and into performance testing of crossbreds, but so far without any startling success. The principle of emphasising selection for the maternal characteristics of fertility and milk production in one line or breed, and the growth and carcass characteristics had been applied in practice for a long time. This does not mean that it is universally applicable. Smith (1964a) examined the theory of selecting specialised sire (for growth rate and carcass quality) and dam (for reproductive ability) lines in pig breeding, but found that selecting for overall performance in a single line produces almost as good results.

The amount of heterosis obtained varies. In some instances, such as beef × dairy crosses, this is but a minor consideration. For milk yield, estimates of 5 to 10% increase from crossing have been made. For mortality and fertility, the increase may be as much as 15%. But the economic value of crossbreds should not be measured only on one character at a time, for many small advantages combine to make a much larger one. How much superior crossbred performance must be to reach worthwhile magnitude is a question with no simple answer, since it is possible to specify husbandry practices and prices for surplus calves, cull cows, milk and milk quality, which when combined would show any breed or cross to economic advantage. Were it possible to rank the several breeds and crosses by efficiency of food use relative to maintenance and caloric or protein output, a sounder basis for choice of a breed or cross might be made.

V. Lethals and Undesirable Recessives

One of the consequences of the spread of artificial insemination has been an increased fear of proliferating lethal genes. "Undesirable recessive" is now a popular term for pathologically abnormal as well as normal but unwanted varieties of new-born animals, such as red calves in black breeds. Many of them, however, have not been sufficiently investigated to be confidently attributed to recessive genes.

Textbooks on animal breeding often contain detailed lists of lethal or detrimental genes. Although undoubtedly useful for some purposes, these catalogues are of limited practical value. It had been assumed by

geneticists, before the mathematical consequences of selection were thoroughly understood, that the presence of lethals in a population presents a growing danger and requires vigorous efforts on the part of breeders to combat it. This, however, is not so. Recessive lethals undoubtedly occur in every species of domestic animal, and deleterious genes of all sorts are abundant. When they are carried in large populations, their manifestation is usually sufficiently rare or they are so difficult to detect as to warrant no action at all on the part of breeders. In small populations, or where inbreeding is practised for the production of lines to be used in crossing, such lethals would become evident very rapidly.

The fear that artificial insemination will spread undesirable genes is not logical. At worst, the bulls used at artificial insemination centres will not transmit more of these genes than the numerous sires they supplant. At best, they may spread many fewer, because bulls known to be potential or actual transmitters are not used. Where a sire has been widely used and later found to be heterozygous for a rare undesirable gene, care can be taken to reduce the risk of using another heterozygote of the same kind in the same area.

It is not to be expected that private breeders will confess publicly that their stock are disseminating a lethal gene, but artificial insemination gives the incidental opportunity to assess sires for such genes, and in large populations even those of low frequency (Johansson, 1961). Commercial dairymen are not slow to complain about deformed calves, and it seems unlikely that artificial insemination will be permitted to spread common deleterious genes very widely. A greater danger might actually be that good bulls are too readily culled on such grounds.

Mason (1964), in a common-sense discussion of breeding policy in relation to recessive lethals, points out that the idea of eliminating them is unrealistic. Whether measures should be taken to reduce the frequency of lethals depends on several considerations: the nature of the defect and the risk to the mother's health, how common it is, and whether any heterozygote advantage is involved. In his survey of artificial insemination practice in nine countries, Mason learned that recessive lethals were a serious problem in none. Sporadic breeding tests are made on suspected carrier bulls but, as a routine procedure, progeny testing specifically for lethals is not operationally sound. It is expensive to organise and can only be used for checking the most feared of all possible lethals. The usual attitude of artificial insemination operators is that any common lethals will advertise themselves among the first few hundred of calves that are bred from each sire in normal use.

An exception to this policy may have to be made if heterozygotes are

found to have some advantage over homozygotes, such as might have been the case with a form of dwarfism in beef cattle (Marlowe, 1964). It would then be sensible to measure the extent of the advantage, to compute the equilibrium frequencies of the undesirable allele, and then decide on operational grounds whether or not steps to discriminate against the recessive are necessary, and, if so, what they should be.

With the evolution of more advanced breeding methods, including the formation of small elite stocks of performance-tested animals, it will eventually be insufficient to apply the present crude custom of cutting the throat of any animal judged guilty of being heterozygous for an unpopular gene. In the artificial insemination of cattle it could happen, and, indeed, is certain to happen, that a suitable progeny test will show that a bull capable of raising production transmits some undesirable trait as well. For a balanced judgment, economic values will have to be placed on his ability to raise the average production of all daughters, and on other characters such as milk composition and conformation as well as on the undesirable trait. To this must be added a clear understanding of its mode of inheritance. Where a specific gene has been implicated, its frequency in the population will be an important factor in estimating the damage a heterozygous bull might do. All animals are known to have some undesirable recessives to pass on, in the sense that they have alleles, which when homozygous reduce fertility, milk production, and vitality (the so-called mutational genetic load). To regard them as a well-defined class of genes and to let their discovery induce an automatic negative mental reaction, is to overlook both biological and financial realities.

VI. Trick Breeding

Generally speaking, genetic methods of improvement of populations have a universality in that they are applicable to all species. Yet there are certain properties of lower organisms and of plants which can be utilised in selective breeding but which are not practical to use in larger animals. Most mutagenic techniques fall into this category. Antibiotic-producing fungi can and have been subjected to irradiation, and mutants for increased production have been selected to establish many commercially valuable strains. Induced mutations have also been successfully incorporated in plant breeding programmes. An early very thorough review of the subject may be found in Gustafsson (1947), while later results have been described by Gregory (1961) and by Gaul (1965). Allied to these methods are techniques of producing polyploidy which are also finding their way into agriculture.

In large animals the situation is not as promising. A limited attempt at inducing useful variation in domestic animals was not particularly encouraging (see Chapter 9). Perhaps the scale of a successful experiment of this sort might have to be prohibitively large. Again, methods for inducing polyploidy in larger animals are apparently not in the immediate offing. Nevertheless, it is encouraging that there is one economically important animal, the silkworm, where some of the genetic tricks, so successfully used for experimental purposes by *Drosophila* geneticists are being adopted for commercial purposes.

Investigations on the genetics of the silkworm have been pursued with great intensity by the Japanese (reviewed by Tazima, 1965). Not only have some 260 genes been studied but of the 28 linkage groups possible, 19 have already been established. Contrary to what has been said about the larger mammals, triploids and tetraploids may be readily produced in this species, and even the problem of the control of sex appears to have been solved (see references in Chapter 9). But the most impressive achievement in the field of trick genetics lies in the development of methods of sex determination of zygotes before the eggs hatch.

In silkworms, males give a higher yield of silk per unit weight of mulberry leaves than females. It is, therefore, of considerable economic advantage to be able to determine the sex before hatching and then eliminate the females. By irradiation, Tazima produced a translocation of a small piece of chromosome 10 to the Y chromosome (in silkworms, females are heterogametic, and hence have an XY constitution, while males are XX). This region carries a normal allele of gene *w-2*, a recessive that causes the pigment of the outer membrane of the egg, which normally darkens after several days, to stay white. The translocation permitted the creation of a strain in which males carry the *w-2* gene on both chromosomes, while females are heterozygous for it. Consequently, in it, dark eggs give rise to females, while light eggs produce only males. An automatic sexing machine has been developed which rejects the female eggs, and thus ensures that only male cocoons are formed.

The same principle has been applied to the problem of recognising the sex of larvae, also of important commercial consequence: since silkworm breeding is based on exploitation of heterosis and, because moths mate very soon after eclosion, it is essential to have an early separation of the males and females.

Techniques of a related kind have been used in poultry. Some breeds, sexually dimorphic at hatch, were developed in the mid-twenties, but autosexing was rendered obsolete by the discovery of a method of determining sex by examining the cloaca of newly-hatched chicks. Genetic techniques of the type depend on the exploration of the effects

of single genes, or chromosome mapping, and on making use of chromosomal abnormalities. For obvious reasons, such studies on large animals are prohibitively time-consuming and expensive. Whether or not this will always be the case, remains to be seen.

VII. Correlated Responses

The idea of correlated responses has always loomed large in the minds of both evolutionists and breeders. This is the phenomenon which Darwin (1872) described under the term "correlated variability" by which he meant "that the whole organization is so tied together during its growth and development, that when slight variations in any one part occur, and are accumulated through natural selection, other parts become modified."

Schmalhausen (1949), among modern students of evolution, has stressed the evolutionary importance of correlation and correlated response and has discussed in detail various mechanisms which could account for it. As noted by Simpson (1953), palaeontologists long ago observed phenotypic associations of characters. But their principal sources, at least so far as artificial selection is concerned, became known only after such genetic phenomena as pleiotropy and linkage were elucidated, even though by no means all correlated responses arise exclusively from them.

One form of correlated response, important in long range evolutionary situations, occurs when an integrated system of organs and functions is disrupted by a novel or increased selection pressure applied to some single trait. Correlated components of fitness then become subject to secondary natural selection pressures working to restore the integrity of the function or organisation of the animal. These components are then brought back into harmony with the shifted property or dimension which was the primary focus of natural selection. As a result of this process, clusters of correlations develop among various characters (Berg, 1961).

The significance of both genetic and phenotypic correlations between traits (for a technical, but reasonably simply stated, model of the relationship between the different kinds of correlation, see Searle, 1961) lies in the fact that usually the expressed desiderata of artificial selection are minimal, that is to say, they involve only a few traits rather than a whole complex including fitness itself. This means that successful selection directed to these desiderata must inevitably produce in its wake undesirable changes in at least those characters which were originally at their optimum. The long-standing problem of quality of

milk has its origin here. Because of negative genetic correlation between milk yield and percentage fat content in cattle (Table 4.2), intensive and successful selection for one of these characters would lead to a decrease in the other. Since the correlation is about $-0{\cdot}5$, it may be theoretically possible to avoid the consequences of the correlation by concentrating selection on those genes which are concerned only with one of the two characters. Since the available genetic variation is then much less, progress from selection would be slowed down.

The complications that genetic correlations can bring about in artificial selection programmes have been discussed extensively for chickens by Dickerson (1955). Because of the intricate network of positive and negative correlations between the variety of traits entering the production of a commercially successful laying chicken, selection directed toward all of these traits simultaneously may be self-defeating. This can happen when, for instance, the selection pressure applied towards trait A is counteracted by the movement of this very trait in the opposite direction as a result of a correlated response to a selection for trait B. Difficulties of this type are magnified by the fact that it is possible for positively correlated characters to become negatively correlated after a period of selection. This process can occur in a variety of ways, including exhaustion of linkage-free additive variation, as has been noted by Lerner (1958).

In the same publication, he has distinguished two types of correlated response: facultative and obligate. The first depends on a purely fortuitous genetic correlation due to pleiotropy or close linkage (the two are virtually impossible to distinguish in higher organisms) between the selected and unselected characters in the initial population. The direction in which the correlated response would occur is here unpredictable. Indeed, in the example of this type of correlated response cited by Lerner (Prevosti, 1955, working with *Drosophila*) correlated responses to the same kind of selection occurred in opposite directions in different populations.

Obligate responses take place in a specifiable direction. They depend on the fact that the traits affected by selection are physiologically or morphologcally in an optimum combination at the initiation of selection. Under such circumstance, it may be expected that reproductive fitness (and hence breeding efficiency in the population) will be lowered as a result of selection, not necessarily immediately, but sooner or later. There are exceptions to this rule, at least over a short range of time: reproductive fitness does not always suffer as a result of selection for some specific trait. One example is provided by the study of Dempster, Lerner and Lowry (1953), who in selecting for egg number in chickens,

did not lower the reproductive fitness of their flock. More recently Rahnefeld *et al.* (1963) selected mice for seventeen generations for post-weaning growth but still found this trait to be genetically positively correlated with litter size.

An interesting case of correlated response was described by Belajev and Trut (1963) in farm-bred silver foxes. In selecting for calm temperament over a period of ten years, they observed a correlated response in the form of prolongation of the oestrus period, which is a highly desirable reproductive trait from the breeder's standpoint. It is not improbable that phenomena of this kind played an important role in the domestication of some of the economically useful animals.

Correlated responses which reduce fitness to the point of near extinction of the population, or, even only to the point of inefficient reproduction, are of serious consequence to a breeder. They are often compounded by the effects of inbreeding, as might have happened in the classical case of the Duchess strain of Shorthorns (Wright, 1923). They can also be independent of consanguinity, as appears to be the case in a selection experiment on shank length of chickens, in which suspension of selection permitted considerable restoration of fitness despite continued inbreeding (Lerner, 1958).

Enough has been said to show that correlated responses have deep practical and theoretical interest. Their bearing on selection limits and performance ceilings is considered in the next section.

VIII. The Costs and Limits of Change

All breeding improvement is founded on the changing of gene frequencies. The aim of the breeder is to increase the proportion of desirable alleles in the gene pool under his control at the expense of the undesirable ones. In theory, the limits of selection on the hypothesis of additive gene action are reached when the desirable alleles are fixed and occur in all members of a population in a diploid state. Beyond this point, all selection can do (unless the objectives are modified) is to continue eliminating undesirable alleles arising from recurrent mutation.

In practice, such a situation rarely, if ever, happens. Some desirable alleles that are originally present at a low frequency may be completely lost by chance from a gene pool. Furthermore, often an allele is desirable or not depending on other genes in a given genotype. Still other genes may display a heterozygous advantage and hence will have equilibrium frequencies somewhere between zero and one and therefore be unlikely to become fixed. However, even with these qualifications, livestock improvement must be viewed in genetic terms as a process

intended to lead to the production of populations with an optimum array of gene frequencies at each locus

It should be apparent that this goal can be attained only at a price, both biologically and financially There are two types of biological costs involved One is based on the fact that, in the replacement of an allele by a more desirable one, many individuals will have to be culled or prematurely removed in choosing animals for reproducing the population This matter is of considerable importance in natural selection, where it has other implications as well It was first raised by Haldane and recently reviewed by Van Valen (1963) The second type of biological cost consists of the loss of adaptation through drift in small populations and through undesirable correlated responses Both types of biological costs result in financial costs But these have, in addition, at least two other components As an extension of the biological costs of the first kind, there are charges against the improvement programme in the form of loss of value of stock which has become obsolete or inferior in comparison with the improved model Secondly, in changing gene frequencies, there are the direct expenses of observation, performance testing and data processing

The immediate question arises then as to who shoulders the burden of money spent on livestock improvement Fanciers may accept a return in the form of relaxation and pleasure, pedigree breeders in the form of sales of breeding stock or the rewards of distinction at shows, large scale poultry enterprises in the form of dividends The only accounting of costs in such establishments is to the shareholders But when stock improvement becomes a question of investment of public funds, a taxpayer might legitimately ask just what amount or kind of change is to be brought about, what for, what will it cost and what will it be worth At the present time, he would receive no answers It is not to be supposed that improvement must be obtained at any price, or even at a stiff price Whether or not it would be a good thing to improve the speed of greyhounds is probably a matter of opinion, but few could be found to say that the cost of doing so should be borne by the public, or even by all dog owners A more penetrating but difficult problem is posed by the beef cattle industry Who should pay for improvements in it? The answer seems likely to vary with political rather than with

question, as we know nothing about the various biochemical, physiological or endocrinological determinants of size and shape in the original canine gene pool. The remoteness of origin, the great supply of variability from hybridisation (Zeuner, 1963, lists five ancestral dog species, not counting the wolves), the sacrifice of reproductive capacity for the sake of fixation of type by inbreeding, the number of generations of trial and error that went into the creation of extant breeds, and similar factors come to mind as partial answers. The question can by no means be considered resolved.

The brief account of the genetic background to livestock improvement that this and the preceding chapters afford will not satisfy those in search of a full exposition of the theory. For them the references will provide guidance in search of further information. The day has long passed, however, when everyone with an interest in some aspect of animal breeding can hope to be familiar with the whole corpus of scientific knowledge pertaining to it. Some things must be left to the experts. On this assumption, the purely genetic treatment of the subject has been curtailed in order to allow more complete discussion of the ways in which science permeates the animal breeding industry.

Part III: The Practice of Animal Breeding

CHAPTER 5

ORGANISATION AND METHODS

Each advance in techniques of measuring passes gradually from being novel to being necessary (Cowan, 1963). This has happened to finger-printing and to blood-typing within the memory of many readers. It is happening to chemical estimates of milk quality and to the measurements of the amount of fat in bacon carcasses. By no great effort of the imagination a student can foresee the day when the elite breeding stocks of sheep will have to be described in terms of their enzymes so that those who breed them for meat and wool can favour the ones with the most desirable properties. For human beings there is already a great mass of information about biochemical individuality (e.g. Williams, 1956) and about its genetic basis (Harris, 1959).

All methods of assessment of performance, including eye judgment of conformation and type, are primarily intended to make a breeding policy effective. However, they quickly tend to generate the very aims of that policy. In fact, if performance testing does not provide or arise from the aims of breeding, it becomes irrelevant as a means. This is an old as well as a very modern problem. In its present form it is created by the setting-up of facilities for the quantitative observation which results in so-called paper records that may in fact be ignored by breeders in the selection of animals. Performance testing under these conditions is make-believe; and yet in a much older form the problem arose as soon as milk recording or egg-laying trials were started. It took a long time before the information produced began to have a significant effect on the ways in which dairy cows and poultry were selected in breeding. Even eye judgment, to the extent that it deals with characters which

There is no case, however, for trying to persuade all breeders in a numerically large breed to take records for breeding purposes. Only enough females must be observed to supply and test adequately the young males from which the sires of the elite stocks are to be drawn. For this the whole population may not be necessary, possibly only a half or less. If an adequate test of a young sire calls for 300 inseminations of herd-tested cows, and ten of them are to be tested each year, some 3000 tested cows are required for this purpose alone. The owners of 6000 more may well feel entitled to the use of already proven sires.

II. Accuracy

Most breeders of livestock have acquired a strong belief in the virtue of accuracy. From their point of view, it is one of the unfortunate aspects of population genetics that it compels an objective approach to the subject.

Reconciliation of the breeders' notions of accuracy of recording performance with those of the statistician and geneticist is often needed. The latter are usually concerned with, and think in terms of, groups of populations. Breeders, like lawyers, tend to consider each animal as an individual with its own special circumstances. The biological apparatus of breeding, however, is designed to deal with populations. Even in poultry, it was not long ago that selection was directed towards producing individuals with record performances. Horse racing certainly justifies this approach. The economics of animal production, however, call for consideration of groups or averages and not of individuals. It comes about, therefore, that scientists try to spend the available effort of observation over the most effective numbers of animals often at the price of reducing the frequency or number of observations on each one (Robertson, 1957).

them on the first two and much quicker. To judge a cow expected to milk for four or more lactations by performance in 70 days of her first one is, in the opinion of breeders, altogether too rough and ready a procedure. But the technical answer to such an assertion is simple. There are three points to it: (a) 70-day yields are quicker and cheaper to obtain; (b) it is better to make progress at the rate of, say, 2% each year than to achieve 5% every four years; and (c) lactation yields or lifetime yields are themselves only rough estimates of a cow's breeding value. Even identical twin cows calved, fed and milked side by side, differ in yield by about 100 gallons and the consequences of varying the season of calving and age at calving would add to this difference. There is no way in fact to find out what a cow's characteristic yield is within narrow limits, though some day, when egg transfer is perfected, her genotype may be assessed through her daughters as that of a sire may be now. The arguments for limiting and adapting the observations on milk yield to the purpose of breeding for milk yield fall to the ground if the data are not used for this purpose or are needed for some other purpose, such as management. The question of paying for them then takes on another aspect.

Poultry breeders have made a close study of the amount of egg recording they should do and in recent years have effected great economies in collecting and processing testing data from birds on test without sacrificing precision of genotypic assessment. Thus not only part-time recording of egg production but also minimal sampling of egg quality (size, shell strength, freedom from bloodspots, etc.) is used. However, heavy dependence on computers by all leading breeding establishments permits them to make the most of the data collected (Dickerson, 1962).

Milk yields and pig performance are approached in a less refined manner and sheep recording is even more primitive. In due course, however, the principles established in the breeding of poultry will have to be applied to the larger animals.

How much expenditure on data collection is justifiable is a question that cannot be given a general or final answer. Methods tend to evolve from the crude to the refined, from the cheap to the costly, as more and more comes to depend on the information. A first trial in a new field of recording carried out on a temporary grant should perhaps aim primarily at becoming accepted. Later on, more or less detail may be found advisable according to the uses made of the information. It is not at all inconceivable that more expense on recording may be required for publicity purposes than for breeding. Touchberry, Rottensten and Andersen (1960), Johansson (1961), and others discuss these

are of very low heritability or even no heritability at all, such as condition, provided information which was quite meaningless as far as breeding was concerned, though, of course, a judge did not think so at the time.

A breeder who records identities and performance has data that are of potential value not only to himself but also to others. The balance of advantage, however, may lie very much to one side or the other. At one extreme there are records that are erroneous, illegible, or not comparable with others. Although conceivably of value to the individual collecting them, they are worse than useless to anyone else. At the other extreme, there are records (as of routine blood grouping), the direct benefit of which to a herd-owner may be negligible.

Since most records are of an intermediate kind on this scale, problems arise in collecting and using them due to conflicting interests. The history of herd testing and egg-laying trials shows how the balance has by degrees shifted away from the individual towards the group to which he belongs. One by one the devices by which poor results could be hidden are giving way to precise methods aimed at obtaining correct information for general use.

I. The Purposes of Recording

The purely organisational aspects of data handling are often confounded by the need for good public relations. Although this fact can be and often is used to delay or prevent refinements, public relations cannot be neglected unless those responsible for animal breeding do not need the cooperation of farmers for identifying and recording animals. The cost of data on the performance of A.I. bulls to A.I. organisations would rise if fewer farmers felt disposed to test their herds for other reasons. If sheep farmers continue to be less than enthusiastic about collecting data on performance, those who would improve sheep will have to find some way of engaging their interest or else build up and pay for breeding stocks themselves as the poultry breeders do. Long established activities such as herd testing which have in the past depended on breeder cooperation, are likely to be the most intractable to modernise. If adequate farmer cooperation is not forthcoming, new forms of organisation for obtaining data will have to be invented. Eventually, information will have to be paid for by those who want it and as it becomes more expensive and complicated to handle, the question as to who really wants it will have to be answered.

To the individual breeder, the value of records may be quite distinct from their value to the organisers of testing schemes, or to research

workers. Farmers unaccustomed to interpreting and using records at the times when they are of significance in husbandry or in breeding may, if they take records, obtain only the indirect benefits that are available to everyone, such as the use of progeny-tested A.I. sires or information from publication of research results. Some may in addition find that recording has a sales value even if the records are otherwise ignored. Thus, any student of milk records can find many herds in which a bull has been allowed to go on siring daughters long after a progeny test has shown that he is depressing yields by 50 gallons or more. With the intensification and higher capitalisation of farming, the proportion of such farmers might diminish as clearer distinctions come to be drawn between records useful in breeding and those with a bearing on efficient management. Breeders who keep no performance records of their stock are, however, still very numerous even in dairy cattle breeding where they tend to be found in the lower strata of the hierarchy. Provided that there is a sufficient price offered by buyers for registered stock without performance records, suppliers will normally present themselves. They will come from among those content with moderate to low levels of management and lacking a wish to have their stock tested or to use anything more than eye judgment in breeding. *There may not be a very promising future for these suppliers of stock;* still none but themselves can be held responsible for misjudging the coming trends. Yet under the pedigree system the number of breeders in the lower strata far outnumber those who are genetically significant. There is, therefore, within breed societies a great weight of opinion and influence expressed by members who have little to gain personally from progressive policies. In the past, this mattered little, since the tempo of change was very slow, but such unbalance hampers the adoption of forward-looking policies.

For breeders, the question whether to test or not is rather complex. The proportion of cows tested for milk yield varies from about 60% in Denmark and Holland to 25% in the United Kingdom, and 15% in the United States. Many factors contribute to this variation, including the warmth of official encouragement. Where performance records are becoming or have become essential for top-class breeding stock, a decision not to test is a decision not to try to produce that class. This has clear implications for the capital value and depreciation of a herd. Testing, however, may show that a herd is of moderate to poor performance and such a discovery would have the same implications. It would not be surprising if, after a little unfortunate experience of testing, some breeders of beef cattle and pigs denigrated it, and proclaimed the merits of eye judgment.

matters in connection with the merits of the special Danish testing stations for the daughters of dairy sires. In the stations the daughter groups can be observed more closely and accurately (at a price) than on their home farms. They can be given known amounts of feed and are readily available as groups for judgments on conformation and temperament. Field data by contrast are less expensive and less accurate in some respects but more plentiful. Furthermore there are difficulties in interpreting the results. Differences between sires are apparently larger and more heritable at the stations than in the field, and the correspondence between station and field rankings of sires is far from perfect. In spite of the fact therefore that the stations exist to assist the selection of A.I. sires, the comparative merits of station data and field data are not to be settled by the heritability of sire differences alone (see section on performance testing in Chapter 4). The vital question is the cost of a unit of progress, and into it will come the amount of selection practised and the information on which it is based. An optimum solution might require a combination of testing methods as well as their refinement to coincide exactly with the realities of bull selection. Where selection is in fact based on numerous criteria, the recording of performance may be mainly of value for farm management, for investigational work, or for watching the performance of an industry, and only to a lesser extent for breeding, since simultaneous selection in many directions is designedly weak in any one of them.

III. Pedigrees

Pedigrees present another source of disagreement about the amount of useful detail. In poultry very little attention is paid to pedigrees and what use is made of them is largely aimed at avoiding close inbreeding. In larger animals there is much variation in the amount of detail shown in herd and flock books: from none at all about females in some sheep flock books to extended pedigrees with performance data on both sides. A common pattern for an individual entry consists basically of an ear number, a herdbook number, and a name of at least two parts (the herd prefix and another referring to the individual and sometimes its male or female ancestors). This is essentially a system of identifying individual animals. Each animal has a number stamped on it or attached to it and reference to this number in a book listing all numbers will give access to supplementary information. Some breed societies no longer publish a herdbook. A filing system and photo-copying provide a substitute. Others face the cost of printing extended pedigrees and long names. What information is wanted depends on who wishes to identify

animals and for what purpose. A policeman looking for stolen cattle, a blood-grouper checking pedigrees, a breeder and a buyer will not think alike. Since breeders, however, design and pay for the herdbooks they naturally use systems which they hope will best serve their needs. Anyone else who uses their systems has scant right to criticise long pedigrees, herd prefixes or lack of legitimate performance data.

Ever since Coates began compiling the Shorthorn herdbook, conscientious efforts have been made by all breed associations to ensure that pedigrees are accurate. As the difference between registered and non-registered animals shrinks, the stratification of the breeding population makes it quite immaterial whether the animals in the lower strata have correct pedigrees, or, indeed, whether they have recorded pedigrees at all. For the business of sire testing no more is needed than a symbol to show what breeding population they belong to, and an identity number listed under their sire and dam. Even in the upper strata where identities and parentages may matter, the usual names have merely the purpose of aiding memory, advertising the breeder, and perhaps indicating membership of some saleable but transient concept of family. Pedigrees, however, still have a commercial value and as long as this remains sufficient, animals will be supplied with them, and money expended on recording, checking, and printing. Expenses of this kind seem to have no direct relevance to livestock improvement. Nevertheless, they may be acceptable as a charge since their existence is implied by the structure of the pedigree system. A social or political decision to support the system and help it to compete in the production of better livestock will entail meeting its costs somehow.

With the advent of blood typing, it has become feasible to estimate rather closely the likelihood that the parents of a particular individual are as stated, provided all three animals are available for testing (Stormont, 1959). Since the tests are expensive to carry out, they will not be requested unless there are compelling reasons. Some improvement in accuracy of recording parents may follow the mere threat of blood typing.

If organised crossbreeding and performance testing expand, those responsible for data processing may find it necessary to devise new systems of identifying animals suited to the uses to which they are put. As distant ancestors, farm and breeder fade into insignificance, corresponding changes in the identification system are likely. A greater use of code numbers to indicate performance, sire, blood groups and locality, and to simplify classification and analysis can be foreseen, since much of the need for identifying animals will come from the recording of performance.

Pedigrees as published have been disparaged many times in the last 100 years or more, but they will continue so long as commercial breeders are still willing to pay for them. Pedigree breeders can be expected to protest that the knowledge of pedigrees conveys much more to owners than the plain recital of names. For them it sums up a breeding programme, and recalls a mental picture of developing animals, their relatives and their circumstances. This may well be so, but the argument weakens if pedigree breeding itself lacks conviction. The test of merit is performance, not pedigree, and it is immaterial what a breeder's methods are if his stock are only average performers.

IV. Publishing

The publishing of data is not undertaken solely because of the use to be made of them but also for other reasons, such as (1) to show that the collecting agency is working in an active and enterprising fashion, (2) to promote research, and (3) to provide an information service for breeders (e g. pedigrees and associated information). In most situations, it is not easy to segregate these reasons, and they also vary in importance. Developmental stages of a new type of recording, for instance, will be followed by routine where research is no longer necessary. Some records, like wool tests, litter records, and milk production data, could be of managerial value to all farmers, others, such as blood groupings, are not. Trimming publication costs is likely to require an assessment of the reasons for publishing when selected data on punched cards or tape are readily available to enquirers interested enough to ask for them.

Although outlays on publishing data are perhaps not serious for publicly financed institutions, they absorb an important fraction of the funds of a breed association. One way of escaping from an ironical situation in which a breed association pays heavily for pretending that all members are important and constructive breeders who must have access to the data, is to encourage the idea that it is proper for the industry as a whole to finance this activity through some separate organisation This is already practised to varying degrees in many dairy industries (including that of the United States) and in the British pig industry. Ultimately, however, even publicly financed institutions may wonder whether it is necessary to publish a great volume of records, including pedigrees, when only a few breeders are able to put it to good use Before selective publication is adopted, it will be necessary to identify these few breeders and their younger replacements. This achieved, it will not be long before the science of breeding becomes as arcane as the art of breeding was before it.

V. Computable Models

Just as growth rate in swine is a character that is changing from being a means to being an end of improvement, so the mechanising of data handling has become a factor in deciding which data to collect and, consequently, which objectives to select for. The essential feature of a computer is speed, and it is therefore illogical to use one unless the result is a worthwhile saving of time, or what is the same thing, money. In due course, the computer may be expected to work out its own diet. Already it is well understood that observations on animals have to be transformed and coded to suit it. The further step of adjusting the frequency, accuracy, and variety of observations to maximise the rate of progress in breeding (Dickerson and Hazel, 1944; Lush, 1945; King, 1955; Robertson, 1957; Lerner, 1958; Smith, 1964; Skjervold and Langholz, 1964) is only a short one for the computer itself to take.

The necessity for giving computers their instructions may provoke more clear thinking about the the objectives of large animal breeding than there has yet been. In industries more advanced in computer use than agriculture, the concept of a "computable model" or mathematical description of a complicated process is commonplace. By means of such a model, the computer can simulate all the components, and if so instructed, actually control the activity at all stages. In genetic research, models have been set up for working out the results of breeding methods and to test complex hypotheses (e.g. by Fraser, 1962).

Production equations and linear programming are by no means novel ideas in agriculture (see Heady and Dillon, 1961) but their practical application is hindered by the lack of operational data. A forward looking industry will need to set up machinery to collect and analyse information on the effects of changing the amounts, for example, of food, or fertilisers, or labour, or breed, on output before it can use computers to the limit in planning.

The highest level of model making yet attempted is the description of the workings of an entire economy (Anon., 1964). Although such a model cannot take cognisance of future decisions of a political character, it can work out the consequences of alternative decisions, provide information on the workings of the system, and expose interdependence and feedback among its elements. Such a development may be a distant prospect for agriculture and for animal breeding, but it may not be long before those with a horror of social planning will nevertheless be glad to see some coordination of the unconnected initiatives now characteristic of livestock breeding.

What has been said about the influence of machines on breeding

applies also to statistical methods. That the problems of animal breeding led Wright, Lush, Robertson and others to contribute notably to the mathematical formulation of the theory of heredity is now a matter of history. For a long time statistical techniques were designed to fit existing practices in animal breeding but the process is now being reversed. Few breeders, for instance, could now expound the theory behind contemporary comparisons, let alone describe varietal types among them (Searle, 1964), but as a result of their use there is a growing tendency to charge the expenses of analysis, and storage of milk yield data, in excess of what is needed for comparing heifer groups, against management instead of against breeding.

VI. Evolution of Testing and Recording Methods

Records serve many purposes which can be condensed into four categories: (a) selective breeding; (b) management; (c) research; (d) publicity.

Some records can be put to all four purposes to some extent but the proportions vary with time and circumstance. What is worthwhile when a recording system is set up may become redundant as the system provides the basic data for its evolution. What is valuable for management (for example, data on fertility or body condition) may be almost useless for breeding. It seems sensible therefore to have recording practices under constant review so that no superfluous data are collected, and no desirable data omitted. Those who do the reviewing should include scientific persons familiar with advances in data handling in population genetics, and in methods of measuring performance. In the past, recording techniques have at times been allowed to become unnecessarily expensive habits rather than sharp tools. To some extent, no doubt, this has been due to neglect, to compromising, and to distrust of scientists. Where recording is subsidised by the general taxpayer there is also a political aspect depending on governmental attitudes to the financial support of farming and especially to the idea that the farming industry is a desirable agglomeration of small units not able

farmers would be willing to finance a new kind of testing about which they knew little. Moreover, developments, such as performance testing of sheep and beef cattle, cannot be expected to begin where herd testing of dairy cows began half a century or more ago. Those responsible will wish to employ the knowledge that has been gained from dairy herd testing and modern data handling and they will want to see the data put promptly to work. Somehow, therefore, they must acquire access to facilities and finance that cannot be provided by a few enthusiastic breeders. Funds will have to be provided by a dynamic livestock industry if the large sums put into research and development by successful industrial companies and the surviving poultry concerns are any guide to economic fitness. It will fall to large scale organisations, no matter whether private or public or hybrid, to accept the risks inherent in new activities.

TABLE 5.1

Types of records

Dairy cattle	Pigs
Census	Census
Pedigree	Pedigree
Colour	Colour
Milk yield	Litter size and weight
Butterfat %	
Protein %	
Type classification	
A.I. conception rates	
Progeny test	Progeny test
(a) on farms	Performance test
(b) in testing stations	growth rate
	food efficiency
	carcass quality
Blood grouping	Blood grouping

No attempt is to be made here to discuss the numerous kinds of data that are collected. A list of some of the commoner categories of records collected from herds of dairy cattle and pigs will serve to illustrate not only the variety of records but also the kinds of techniques and technicians. Table 5.1 has been compiled in descending order in such a way as to show roughly how data range from mere enumeration to the intricacies of blood grouping; how the number of stock owners directly

interested grows smaller; and how the observations require increasing skill and large scale organisation. Since the list is also approximately in order of practical application, it indicates how the methods used by pig and dairy cattle breeders have been modified over the last fifty years.

VII. Evolution of Breeding Methods

The evolutionary trend of breeding procedures in livestock seems to start with local populations of animals which develop a cohesion and later on a breed society or its equivalent. These breeds were often and possibly always built up on a crossbred foundation just as were the new breeds of more recent origin.

The second stage of the process is intra-breed selection which comes when there is agreement on the objectives to be sought in breeding. At the same time as this intra-breed selection is going on, there is a between breed selection which reduces to virtual insignificance all but a few prominent breeds.

The third stage is the appearance within the dominant breeds of strains, sub-populations or isolates which lead to intra-breed between-strain selection, as a result of which, most of the strains are gradually eliminated.

The fourth stage of the process is the inbreeding of these strains accompanied by a further stage of sub-division so as to make a number of inbred lines. The inbred lines in their turn are subject to the same selection, either pure or in crosses. The surviving inbred lines are then exploited in the form of line crosses involving two, three or more of these lines.

In the United States and the United Kingdom sheep and cattle are predominantly at stage two, pigs are moving towards stage three, and poultry have reached stage four. Organisation has to develop to permit moving from one stage to another

A rough comparison of the major classes of farm livestock is given in Table 5 2. It is intended to apply to both the United States and the United Kingdom but fits neither exactly. How extensively a technique must be applied to rank as "widely used" is of necessity quite arbitrary. The main differences, however, in both purebred and crossbred populations are perhaps clear enough Poultry have a strong lead in organised crossing of selected strains Because they are individually of small value, are readily kept in large numbers, and multiply rapidly, they are relatively easy to mass produce. Given mass production, better breeding systems can be designed It is not a question of a special genetic situation; for there is nothing about their heredity to distinguish poultry

from other animals. In all of them size and growth rate are moderately highly inherited as is the fat content of milk or meat. Fertility and viability are generally of low heritability within breeds or lines as Table 5.2 indicates. The heritabilities shown there, it should be pointed out, are merely round figures representative of published values.

TABLE 5.2

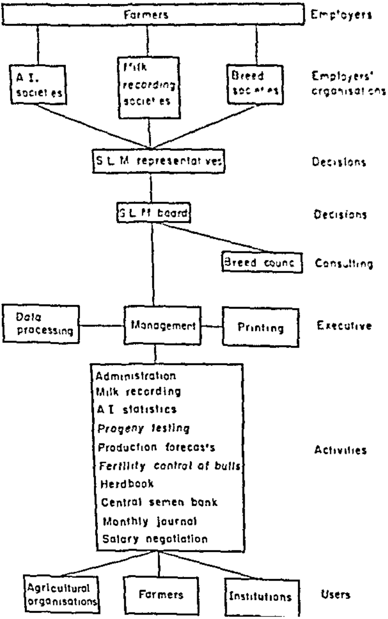
A comparison of the main classes of farm livestock
X = *widely and effectively used;* ⊗ = *minor use as yet*

		Dairy cattle	Beef cattle	Pigs	Sheep	Poultry for eggs	Poultry for meat
Closed population	Eye judgment	X	X	X	X		X
	Breed Society	X	X	X	X		
	Performance test	X	⊗	X	⊗	X	X
	Artificial insemination	X	⊗	⊗		⊗	X
	Family testing	X		⊗		X	X
Organised crossing	Eye judgment	X	X	X	X		X
	Performance test			⊗		X	X
	Large scale breeding			⊗		X	X
	Inbred lines					X	⊗
	Control population					X	
Approximate heritability	Amount of product	30	40	40	35	20	40
	Quality of product	45	30	50	40	50	30
	Reproduction and viability	5	5	10	5	10	10
Ranking	Value of individual animals	1	1	3	4	5	5
	Reproductive rate	5	6	3	4	1	1

VIII. The Handling of Records

The methods followed in different parts of the world to integrate the handling of records show much diversity. Some idea of it can be acquired from a small selection of countries with dairy industries. In Scotland, the functions of collecting milk yields, analysing them, using them for choosing and culling bulls for artificial insemination, and keeping pedigrees, are carried out by four independent bodies which collaborate as and when they feel disposed. In England and New Zealand, all these functions, except pedigree registration, fall to the Milk Marketing Board, and the Dairy Board. Details of organisations in fifteen European countries can be found in O'Connor (1962). Breed

improvement in the U.S.S.R. is implemented by the State Department of Inspection for Breed Improvement and Herdbooks. Its functions



a summary of breed performance. Scientific institutions are charged with raising productivity, improving existing breeds, and making new breeds, and it is from the broad ties between agricultural science and practice that the successes of animal breeding in U.S.S.R. are believed to have come.

Integration has been achieved in Sweden in another way. Figure 5.1, adapted from *publicity material of Swedish Livestock Management*, shows how the several farmers' organisations interested in milk records and breed registrations have combined to form a board which carries out on their behalf a wide assortment of activities ranging from herd

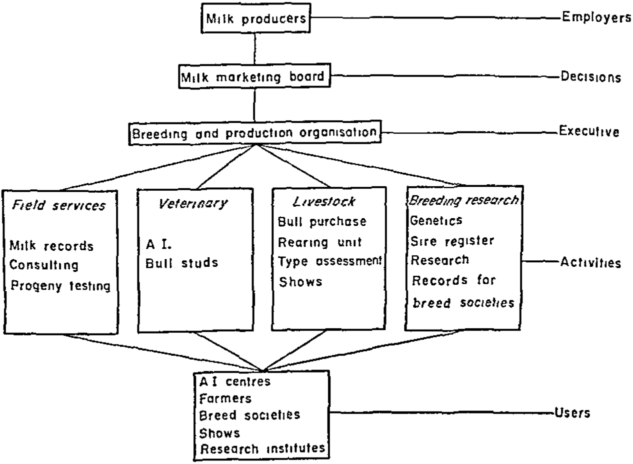


Fig. 5.2. Breeding and production organisation of the Milk Marketing Board of England and Wales.

testing to publishing herdbooks. By so doing, it relieves the farmer organisations of technical supervision of staff, computers, printing and other specialised processes. They have, of course, to finance it, but by combining they achieve more at less cost than they could by independent action. Apart from pedigree registration and publication, the English arrangements have much in common but they are achieved through a milk producers' board (Fig. 5.2). Trends in all countries are

away from the original simple herd records that were left in a raw state for the farmer to interpret as best he could. There are several reasons for this. The needs of the artificial insemination industry for data in bull performance, and the exigencies of research on the characteristics of cattle, individually and in groups have brought about the use of expensive machines to cope quickly with incoming data. Almost as a by-product, the herd-owner benefits by a faster service, more detail, and statistics which enable him to compare his herd with those of other owners.

IX. Organising Breed Improvement

In this chapter, so far, certain aspects of the technicalities of recording data to be used in breeding plans have been discussed at the level of the farm or breed society, or of a small co-operative. For a government or an industry there are other considerations which are rarely ventilated, although they must have arisen in Scandinavian countries with highly integrated livestock industries.

Comstock (1960), in discussing breed structure in pigs, illustrates some of these problems. He begs the question of how to maximise selection within purebred populations by assuming that pedigree breeders will continue to be an essential part of the process, in spite of the fact that they are mainly concerned with their own financial advantage and not with maximising selection. However, within this context, he considers what could be done to improve progress on the premise that selection within breeds is far less effective than it could be. Market hogs in the United States are mostly crossbreds derived from purebreds and their standard of performance is therefore dependent on the standard of the purebreds. On present evidence, swine could be improved fairly quickly in carcass quality, but selection for litter size, growth rate and feed efficiency has been disappointing, and the outlook is unpromising.

Comstock proposes the following methods of dealing with the problem of improvement:

1. a more extensive study of crossbreeding and a determined search for breeds that cross well;
2. more intensive selection within purebreds;
3. more research on the improvement of the parents of the crossbred, known as selection for combining ability;
4. new breeds.

All these proposals have led to some action in the past but not enough. Initiative is still needed on a large scale and in places where it matters.

A vast comparison of breeds and crosses is conceivable if the facilities and personnel could be drafted to carry it out. More intensive recording of herds and larger selection differentials are possible but unlikely unless

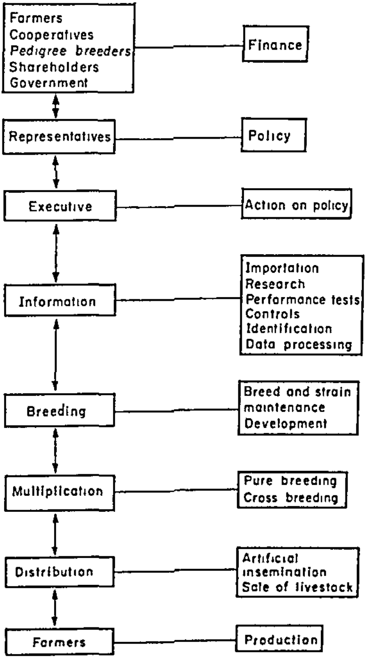


Fig. 5 3. Essentials of industrial organisation of breeding.

industrial scale. Obviously, a breed association of the traditional kind will not suffice. Something new is needed. It could develop out of existing associations, or from new ones such as the Performance Registry International which encourages performance testing of beef cattle in the United States. Dairy boards and artificial breeding

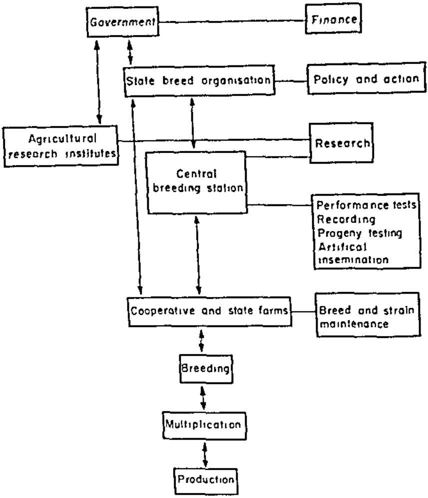


Fig 5 4 Organisation of animal breeding in Czechoslovakia (based on Šiler, personal communication).

organisations might establish their own testing, pedigree registration and breeding departments The existence of such a body or bodies is no assurance that a policy will be laid down and the finance provided; but its absence means that there will be neither. Whatever the precise origins and characteristics of the system adopted, it has to provide the essentials of the industrial organisation of breeding as shown in Fig. 5.3, more fully discussed in the section on integration of services (a

comparable diagram for a Central European socialist state is shown in Fig. 5.4).

In the United Kingdom a Pig Industry Development Authority was established in 1957 and financed by a levy on carcass meat. The Authority, now to be absorbed by a Meat and Livestock Commission, consists of seventeen representatives (two for pedigree breeders, four for commercial producers, one for agricultural employees, two for bacon producers, one for bacon distributors, two for distributors of fresh pig meat, one for manufacturers of pig products other than bacon, one for employees of processors, marketers, and distributors of pig products, and three independents) and their function is to promote breeding, production, grading and marketing. Of Comstock's four proposals, which have as much validity in the United Kingdom as in the United States, only one has so far received substantial attention from the Authority. Efforts have been made to encourage progeny and performance tests; and the next step is to persuade breeders to apply the data to selection (Smith, 1965). As logic requires, there is a plan to build up a new stratification of the breeding population based on performance testing to replace the old one based on official breed type. But it is a slow process. Enough breeders and the necessary buyers of stock have to be weaned off the old system to make the new one viable.

Although individual members of such an Authority may be enthusiastic about their duties, if they represent diverse interests within the industry, their net effectiveness may be small. Sceptics would wait to see whether, having willed some of the means of swine improvement, the Authority also willed the ends.

X. Local Varieties and Importations

As the speed of transport has arisen, the idea of a locally adapted breed has tended to change. For the purpose of animal breeding, the size of a locality has been growing until whole countries have to be regarded as mere localities. Wise as it may be to look askance at claims of special adaptation to local circumstances (for instance, breeds of beef cattle, such as Welsh Blacks and Highland cattle are characteristic of certain regions, probably more because of tradition than of any biological peculiarities), it should be remembered that at least some forms of local adaptation are bound to have a genetic basis. Evidence of gene-controlled aberrations of metabolism, and of hereditary variation in susceptibility to deficiencies of diets and to infections (Hutt, 1958) is abundant. Progress in nutrition and veterinary science will find ways of adjusting environments to avoid exposing genetic weaknesses,

but there remain local hazards of heat and cold, food supplies, and diseases (note postulate 5, in Chapter 3) that will require locally adapted stock, especially when extensively kept.

Breeds of domestic livestock, and man himself, have flourished under many environmental conditions. The Americas, Australia, and New Zealand have all founded their livestock industries on livestock from the Old World. Even in Britain, there may be no significant breed to-day that is not wholly or partially of immigrant origin within the last 200 years. In recent years, the introduction of Landrace pigs and Friesian cattle has been of benefit both directly from their performance and indirectly by the stimulus to pig and cattle breeding. There are good reasons therefore to exploit and rationalise the exchange and testing of breeds and crossbreds between countries as suggested in Chapter 8 (see also articles by Lush and by Phillips, in Hodgson, 1961). In the not very distant future there may well be international centres or schemes for comparative trials.

Migration works best when stock moves towards better conditions as in stratified sheep industries. In the reverse direction, adaptation takes longer. Although the prospects of obtaining new and desirable genes from really exotic varieties may glitter, they may be a long way off. History gives many warnings against too great an optimism in this respect. The failure of British breeds to establish themselves in India and other tropical countries has not been for want of trying, nor has the failure of the fifty-year-long attempt to develop a hybrid of cattle with buffalo that would show improved hardiness and productivity in Northern Canada.

For the winners of the battle of intensively reared breeds, a world market is the prize. Livestock industries, if they enter this battle, need to be organised accordingly. It will not be won by advertising unless backed by convincing performance data. The other side of this coin shows that, unless protected by regulation, local or national breeds will be subject to competition from abroad. This should encourage animal breeders in one country to match improvements in other countries, but, in spite of the historical evidence of the value of importations, their beneficial influence has been allowed to work only sporadically in the past. Until Charollais bulls were brought to England in 1961 and given an extensive trial by the Milk Marketing Board with the aid of artificial insemination, no adequate test of an imported breed had ever been conducted in Western countries. Even this test was conducted only on crossbreds Still, as the successful emigrations of many breeds of livestock have already shown (for examples, Jersey cattle, Merino sheep, thoroughbred horses and United States-bred poultry), breeds in

possession of a territory cannot rely on their adaptation to local conditions to protect them from invasion from abroad. In addition to being adaptable, the invaders may be supported by good records of performance and the power of big business.

XI. Integration of Services

A fully integrated scheme for the breeding of livestock would, on present knowledge, have the basic structure shown in Fig. 5.3 which puts in diagrammatic form the stage which has already been reached in advanced industries. It also exposes the points at which the less advanced industries have fallen behind. How quickly these can catch up is a matter of political and social attitudes to change and they are not the same in all countries or for each type of livestock. The arrangements for obtaining finance and determining policy are crucial since all the rest flows from them. In the figure, five separate possibilities for ensuring the necessary financial basis are shown. These are not intended to be mutually exclusive or to be exhaustive. If, however, the finance and policy are provided by a single corporation (for example a dairy board, an artificial insemination organisation or a government), all stages of the process of breeding and distribution of livestock would be influenced, if not wholly controlled by that corporation. All its costs would ultimately have to be paid for by those who bought commercial stock as semen or as animals, or by the general taxpayer.

It will be observed that this scheme is not dependent on the improvement achieved in the course of breeding of livestock. In this respect it does not differ in any essential from the pedigree system (which is included in the figure). The main deficiency of the pedigree system is that it is inadequate with regard to finance and policy. In consequence, the activities described as information and breeding fall short of national needs in objectives and in scale.

As mere providers of services, breed associations seem to have a rather uninspiring future. If they can make the transition to organised and centrally directed breeding, they will be users of services (and scientists) and will be competitive with other large organisations. This seems one way to exploit the skills and interest of the individual breeder as well as to provide insurance against the possibility that the large breeding organisations will become as conservative as breed associations are now. Whether or not breeders collectively accept this challenge, the stratification of animals by performance is bringing out a new class of elite breeder and, thus, of breed society administrator and councillor. Funds will be increasingly diverted towards performance

trials and the incidental costs, and away from the lower ranks that contribute no genes to subsequent generations. No doubt such a metamorphosis of breed societies would offend some of their members, who might prefer to stifle competition in their old sphere of influence in animal breeding, exercise an authority they do not possess, and enjoy a status they have inherited But the younger members will sometimes risk this disapproval.

If applied research and development become a charge on the industry which profits by them, they should include organised comparisons of breeds and crossbreds Breeding institutions could use this kind of service in the making of the new elite and multipliers' herds based on performance, and possibly inbred lines, or lines developed by recurrent selection Should control of genotype-environment interaction also yield to research, another need may arise for specialised lines and the services required to keep and exploit them.

On a longer view, genetical engineering and euphenics (see Chapter 9) will also fall into this category. Meantime, however, the manipulations of the physical basis of heredity and the biochemical adaptation of environment to extract the best out of existing genotypes have still to be achieved by research workers Meantime, also, the industry still awaits the application of computer technique to comparatively small scale enterprises, as, for instance, to a single breed association running a cooperative breeding venture, and using a miniature computer for drawing instantaneously on a central fund of knowledge of markets and their effect on breeding aims, as well as of performance tests. It may not have to wait much longer.

CHAPTER 6

EVOLUTION OF LARGE SCALE BREEDING

The development of breeding methods did not proceed synchronously in all classes of animals. However, until recently, the histories of breeding of the various kinds of livestock were similar enough to allow a rather general survey to be made for all of them.

I. Historical

From Aristotle onwards, animal husbandmen have never been at a loss for theories on breeding. Berge (1961) has traced them with a touch of humour and a fine detachment. At all times there have been great authorities and from them or their followers it is possible to learn how the doctrines of breeding have changed since the Middle Ages. It is convenient to begin with the coming to Britain of the Arab horse in the seventeenth century. About this time, breeders, after having crossed the imported horses with those locally available, adopted a belief in purity of pedigree. Then there were Buffon (1708–88) who advocated systematic crossbreeding, and Candolle (1778–1841) who thought that some parts of the body were governed by the dam and others by the sire.

Bakewell (1725–95) and others of his day do not seem to have been much influenced by earlier authorities but they laboured with clear objectives and strong selection in a population with plenty of genetic variation. Bakewell was a pragmatic sort of man, a man of methods rather than of principles. Authors who reported on his methods were obliged to infer his principles from his practice since he made no statement of them himself. It has been said (as quoted by Youatt, 1834, p. 101) that he based his work on choice of breed, beauty and utility of form, texture of flesh and propensity to fatness, and gave effect to it by mating like to like, even if related. Until recently, many a

breeder of meat animals would have subscribed to this philosophy. It hardly amounts to a revelation of breeding secrets, and this is small wonder, for Bakewell could have had none. His friends provided him with some Emperor's clothes that have worn well. One far-sighted writer, however (see Youatt, *loc. cit.* p. 192), commenting on Bakewell's passion for early maturity, small bones and thick layers of fat observed that "Having painfully, and at much cost, raised a variety of cattle the chief merit of which is to make fat, he has apparently laid his disciples and successors under the necessity of substituting another that will make lean." It is as true now as in the eighteenth century that those who breed the elite and significant animals are but products of their day and generation. Their aims are bound to be superseded but no one knows by which others for there is no predestination in evolution.

In 1794 George Culley reflected "Could any of these people be prevailed upon to make an experiment, they would most probably find that excellence does not depend on the situation or size of horns, or on the colour of faces and legs, but on other more essential properties." He would find that although this is now known, it is also known to be an expensive and possibly unrewarding business for the unaided breeder

still being used (Briggs, 1958). As with the preceding notions, this one had elements of truth in it, which are referred to now as homozygosity, dominance or epistasis according to the kind of gene action involved. Erected upon this rather small foundation, however, were some theories about the prepotency (and thus the desirability) of particular animals, or breeds, which seem likely to have transcended the reality or else to have misinterpreted sampling errors.

In 1859, Darwin published "The Origin of Species", and in 1865, Mendel the results of his studies of inheritance in garden peas, but they had no immediate impact on animal breeding. Galton (1822–1911) was also ignored, although his quantitative approach to variation among relatives could have been valuable. That had to wait for Fisher, Wright, Haldane and Lush in the period 1918 to 1939.

While the founders of modern population genetics were being disregarded, breed societies and herdbooks were growing in strength. Studbooks began with the first volume of the General Stud Book for horses in 1808, and was followed by the Coates Herd book for Shorthorns in 1822. During the next hundred years many more were started. Mason (1957) names 24 cattle breeds, 16 pig breeds, 21 horse breeds and 33 sheep breeds in Great Britain (Colburn, 1963, lists 43 breeds of sheep). In the United States of America there are almost as many. Rice *et al.* (1957) give the addresses of many Livestock Registry Associations· 25 for cattle, 16 for swine, 22 for horses and 25 for sheep. Most of these societies or associations still subscribe to the principle that pedigree allied to the use of eye judgment for securing adherence to formalised breed type is the basis of successful breeding. This formalistic approach is intellectually related to the typological view of systematics. For the typologist the type is real and the variation an illusion, whilst for the populationist the type (average) is an abstraction and only the variation is real. Replacing the static idea of type by the dynamic notion of an interbreeding population moving erratically and at changeable speeds towards an unknown future is ranked by Mayr (1963) as perhaps the greatest conceptual revolution in biology.

The beginnings of systematic research on the genetic aspects of animal breeding are of recent origin. Important as they were in moulding the thinking of breeders, the Pennycuik experiments of Cossar Ewart, carried out in the period 1896–1904 do not really fall into the stream of genetic research on methods of animal improvement. In fact, considerable strides towards attaining today's standards of excellence in many kinds of animals were made in pre-Mendelian days, and it may be said that there was genetic research before genetics itself was born. The roots of research in animal breeding are to be found in empirical

observations and field trials long before theoretical foundations for them had been laid.

During the late nineteenth century, attempts to measure the success of mass selection in raising egg production in poultry and the experiments on the inbreeding of guinea-pigs, started shortly thereafter by the United States Department of Agriculture (very likely the first use of laboratory animals as pilot subjects for studies specifically directed towards animal breeding), were initiated outside the framework of Mendelism. Nevertheless, they can probably claim to be the earliest systematic efforts to investigate the genetic basis of animal improvement. The rediscovery of Mendel's laws in 1900 had a stimulating effect. The relative ease with which Mendelian inheritance could be investigated for truly monogenic situations and the unbridled opportunities for invoking various types of gene interactions in studies on polygenic characters allowed a great deal of experimental work to be done. Some of it was useful.

It was, however, the coming of population genetics which gave the greatest impetus to the development of animal breeding investigations. Though the foundations of the theory and analytical methods of population genetics are usually attributed to the trinity of Fisher, Haldane and Wright, it was the last who played the most important role in bringing quantitative genetics into livestock improvement. Not only was he himself active in animal breeding (having served as Animal Husbandman in the U.S. Department of Agriculture before becoming a Professor of Zoology), but it was his formulations upon which Lush, the greatest exponent of this approach, built.

The influence of Lush on the development of animal breeding research can hardly be exaggerated. Since the first appearance of "Animal Breeding Plans", hundreds of investigators trained directly under him or under his students, have followed his lines of research. Probably no research institution in the Western world which deals with the genetics of domestic animals lacks one such worker. Contributions from the school of Lush have been many and significant both from the theoretical standpoint and in application to breeding of all classes of livestock, poultry, and more recently, fish.

It was not only because it elaborated the inheritance of continuously distributed traits that population genetics became important. At least two other factors played a highly significant part in the spread of this school of thought. One was the possibility of generalising the theory of quantitative inheritance and so justifying the wider use of rapidly breeding animals such as mice, rats, *Drosophila*, *Tribolium* or quail for reaching conclusions relevant to larger animals. The other factor was

the development of statistical analysis which could be applied to existing accumulations of data. For some purposes it was therefore unnecessary to wait for several generations of breeding.

An attempt at summarising recent evolutionary history of swine breeding has been made by Comstock (1960). His choice of important developments during the last century will serve for all classes of stock.

1. Formation of standard pure breeds and registry associations.
2. Development of Mendelism and population and quantitative genetics theory.
3. Recognition of the value of cross-breeding.
4. Renewed breed formation and the founding of the Inbred Livestock Registry Association.
5. The shift of emphasis in selection to economic traits.
6. The analysis of selection effects.
7. Measurements of backfat on live hogs.

Other compilers might make a different and shorter list. The next two items on his list could be the general adoption of performance testing for breeding stock, and the building up of large breeding populations under unified control.

II. Functional Stratification

Large scale breeding, like any other significant evolutionary or cultural change, can only take place when the circumstances are right for it. In a complex industry, such as livestock production, a change of this order causes repercussions in many directions and calls forth strong reactions. For understanding recent events and for assessing their influence, it is as well to consider briefly the existing organisational structure and the modifications of which it is capable.

There are now three kinds of functional stratification in animal breeding that are easily recognised. Firstly, there is stratification on the basis of geography and land use (Nichols, 1957; Epstein, 1965). Secondly, there is stratification by repute, namely breeders of elite herds, multipliers and users of non-registered stock (see Chapter 7). Although originally this kind of stratification was based, or was intended to be based, on the performance of animals, it has gradually come to apply to the performance of the breeders themselves. Performance stratification is now being re-established as progeny testing and selective breeding from proven sires lead to the formation of highly selected strains and derivatives of varying degrees of relationship to them. There may well be a fourth type of stratification in the near future if

minimal disease or specific pathogen-free stocks of animals prove to be economically justifiable.

The importance of geography and land use depends on the kind of stock. Owing to the bulky fibrous food they graze, ruminants are more affected than non-ruminants. Technical control of environment, however, influences even ruminants under extensive conditions. Housing and feeding, the supply of minerals and vermifuges, and intensification generally make the relationship between land and climate and between land and breed less important. Both the need for and the speed of adapting stock to new intensive forms of production are greater than for extensively kept or range stock. Altering the genotype of range sheep or cattle may be a risky proceeding if the physiological nature of adaptation is not known. This is also true of animals for intensive farming, but it may be easier to adjust the environment if the stock prove deficient in some respects. Long continued selection under range conditions has produced genotypes that in some ways are well suited to intensive conditions, for example, in fertility, temperament, or fleece type as the use of range or hill ewes for lowland crossing shows. In other ways, however, they may have become unsuitable, notably in growth rate or conformation.

Dairy cattle, pigs and poultry are reared under a wide variety of conditions, a variety that is probably greater than is realised, since so little is known of the minor challenges to health faced by livestock. Sheep are still markedly regional in distribution (see Portal and Quittet, 1950, about France, and Lall, 1956, about India) Tradition is important here, but adaptation by physiological or psychological means such as temperature regulations or behaviour in bad weather respectively, may sometimes be critical. In contrast to the merino, which apparently has a compulsion to go on producing wool protein even when underfed, other breeds, at home in regions where a regular winter shortage of food coincides with pregnancy, may be found to reduce wool production and to exploit protein catabolism to help them survive.

To many people the most striking effect of geography and land use is to be seen where intensive cropping excludes all livestock. But the classical form of stratification is shown where sheep migrate from less to more productive land and change from purebreeding to crossbreeding in the transition (Fig. 6.1). The eastward movement of Western ewes for crossbred lamb production in the United States, and the downward movement of ewes in Britain from poor hill grazings to land capable of producing fat lambs are well-known. An extension of this system has been forecast for the supply of suitable ewes for indoor production of lamb on the principle that the breeding ewes should be

reared on land that is cheaper than the land they are in turn to rear market lambs on.

To unite the advantages of cheap breeding stock with the higher performance that their offspring can show when food supplies are more liberal, it is necessary to use suitable rams. They must combine with the ewes in such a way as to produce a crossbred lamb appropriate to the market. *Consequently, they need to be complementary to the ewes,* rather than excellent in themselves. To meet varying requirements there is a range of breeds specialising in the production of these sires of which the Hampshire and the Suffolk are examples. Extremes of size are to be had in the Southdown and Oxford, and an extreme in wool

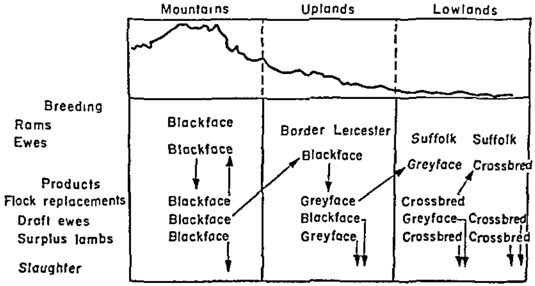


Fig. 6.1. Diagrammatic representation of breed stratification in the sheep industry of Scotland, based on the Scottish Blackface and its cross progeny, the Greyface.

numbers of draft ewes from the hill land are well balanced with the demand from low land and have at no time far to travel. These draft ewes become dams of crossbred ewes sired mostly by Border Leicester or Suffolk rams as is shown diagrammatically in Fig. 6.1. Apart from heterosis, the object of the crossing is to produce a ewe that has the size, fleece, fertility and milk production needed in the mother of a fat lamb. It might be hard to find a more complicated task than improving the sire of such a ewe. Yet it might not be wise to be intimidated by it since changes in just one trait might be useful. The real problems are to define the aims and to obtain the necessary data.

Two forms of stratification by performance have appeared since the war, and both are the products of research. The first arose from the organised crossing of inbred lines of the same or different breeds of poultry in one or more stages to produce the final broiler or egg-layer. Although comparatively poor performers themselves, the inbred lines merge successfully in the making of birds that accurately meet specifications, which may include failure to reproduce. Dairy cattle are far from emulating poultry but are nonetheless near to establishing the second form which is a ranking on the basis of their relationship to outstanding sires found by progeny testing and artificial insemination. Now that it has been shown that the most likely source of good bulls is the offspring of proven sires mated to daughters of proven sires (Robertson, 1960a, Carter, 1962), it is a short step to segregating (on paper and on farms as well) the animals which meet these qualifications. Together with their descendants they can be maintained by a continuation of the same process. With several such groups, independent regional policies can be followed. If these policies result in the creation of a set of sub-breeds or lines within a breed, then organised crossing between lines becomes a possiblity as well as the classical inter-group selection process.

may be different from those which will be important in larger animals. Artificial insemination, for instance, a powerful influence in this direction in cattle, played no significant role in the poultry revolution. But the basic causalities are the same and spring from the necessity for greater efficiency in food production, as outlined in Chapter 2.

As late as the beginning of this century poultry breeding as a business was oriented primarily on poultry shows in which merit was judged by conformity to the breed standard. Commercial qualities of poultry were not being measured precisely and contributed very little to the standing of a breeder as a source of stock. There was a great number of different breeds and the numerous breeders propagating them had their reputations established almost entirely on winnings at poultry shows. Most of them were back-yard fanciers, and poultry for food production was only a part-time occupation which provided pin-money for the farmwife. Little by little, however, commercial exploitation of poultry as an important source of food began to develop. Following the invention of methods for storing, packing and distributing eggs, specialised egg-producing farms began to arise. Shows still dominated breeding but, in addition to classes judged on breed standards, so-called or miscalled, utility classes were introduced. In these, merit was measured on certain assumed relationships of physical appearance to production qualities, relationships which later were demonstrated to be fallacious. An even more important development was the spread of egg-laying tests in the nineteen-twenties and thirties. These existed in two patterns, based either on the production of individual birds, or on the production of pens of ten to thirteen pullets, entered by breeders in contests conducted by state agencies at central locations. Individual performance was recorded for a year by trapnesting. The breeder himself decided what birds he would enter in a test, the only qualification for entry being conformity with the breed standard. The ranking of competitors in a test was determined mainly by the number of eggs laid by a pen and replacement of birds dying in the course of the test was often

test winners themselves. Great emphasis in such sales was placed on pedigrees and on even remote ancestors.

In the nineteen-twenties and thirties, recording schemes, or record-of-performance tests on the breeders' own premises under Government inspection, were started. Not only conformity to breed standards but also certain pedigree requirements were instituted as conditions for entry. Adding egg size to the qualifications for certificates of performance also characterised this stage. Disease control, especially of pullorum, carriers of which could be identified by agglutination tests, was also introduced as a condition of official recognition of breeding and production quality.

Meanwhile, the perfecting of mammoth incubators, the introduction of mail shipment of baby chicks, and the building of large plants for the commercial production of eggs supplying the increasing urban population, led to a stricter competition between breeders themselves, and also made them direct competitors of the previously existing middlemen· the multipliers and hatcherymen. Eventually both of these classes disappeared from the stage as independent operators. Their functions are now performed either by the breeding establishments themselves or by subsidiaries working on the franchise or licence system in which the immediate parents of chicks supplied to the customer are produced under the supervision of the licenser. Indeed, the majority of the breeders who survived this change and stayed in the

need for objective measurements of economic worth of the actual product sold and not of breeder-selected samples tested in the standard egg-laying test; (3) the development of the hybrid and crossbred fowl, which spelled the death of breed standards in commercial industry; (4) the self-accelerating phase in the growth of individual establishments and the accompanying reduction in their number.

The *stimulus to employ professional geneticists arose from the* desire of a few pioneers who wished to put their selection and mating procedures on a firm scientific footing. It was John Kimber of California who over a third of a century ago foresaw the future of commercial poultry breeding enterprises as big business with a scientific approach in every step of operation. The success and rapid expansion of his firm, in part due to the methods he adopted and in part, of course, to his personal managerial ability, has led others to accept his philosophy. In the early years of this development, commercial firms raided universities and experimental stations for staff. Certain changes in post-graduate training to supply the new market for the industrial geneticist (openings heretofore restricted to plant breeders) also occurred. At present an equilibrium probably exists. Since the number of independent breeding establishments has been drastically reduced, the total number of geneticists employed by the industry is probably no longer increasing rapidly.

The rise of the random sample test deserves notice. The principle is to test for production qualities large samples of the actual stock that is being offered for sale by a breeder, rather than to evaluate selected small groups chosen by the breeders themselves, groups which may have no genetic relation whatsoever to the birds being supplied to the customer. Random sample tests had been advocated by Hagedoorn (1927) for nearly twenty years before they came into existence in America. Shortly after the last world war an experimental random sample test was organised in California through the initiative of poultrymen, breeders and experimenters. The system has gradually spread throughout the United States and Canada. Whatever the original purpose of the random sample test, it had a considerable effect on the structure of the poultry industry by leading to the virtual extinction of the small breeder. What happened was that *customers tended to take the published results of the early random sample tests too literally* and accepted the ranking as measuring the exact order of genetic merit of stocks offered for sale by the various entrants. This meant that, if, by chance, a small breeder did not gain a very high place in the test (even if this reflected only an environmental component in the performance of his stock), he could lose so many sales to his larger competitor that he

could not survive. In contrast, a large breeder with capital reserves could afford to contract his business temporarily if he did not succeed in a test in one year, and later expand rapidly so as to capitalise on a chance win. The process of breeder extinction in the manner that statisticians call a random walk was thus initiated.

Attempts to reform the tests so as to make them less of a competition and more a quality control measure (for example by issuing labels to breeders meeting certain standards without necessarily publicising their actual performance or rankings) were only partially successful. Dickerson (1962a) has reviewed the changes which have occurred in random-sample tests since their inception with respect to their avowed purposes, their numbers, their reliability, and the eventual use of information obtained from them. These tests are expensive to carry out, and the justification for them must vary with the stage of evolution of a poultry industry. When there are numerous breeders and breeding stocks of unknown merit, the tests perform a valuable service in comparing them under standard conditions. As time passes and the surviving stocks become closely similar in estimated total economic returns (less feed and chick costs), it grows progressively more difficult to identify superior lines, notwithstanding larger samples and repeat tests in several states. Furthermore, influences other than genetic merit, such as transport costs, advisory services, and personal contacts, play an important but imponderable part in determining a buyer's choice. The random sample test helped to establish the crossbred chick and the large scale breeder, but having done so, it needs a new purpose if it is to survive in North America Elsewhere, its value is for the time being more apparent.

The increased utilisation of crossbred or hybrid (a cross between two inbred lines of the same or different breeds) has had a tremendous impact on the poultry breeding industry. Byerly (1964) estimates that two-thirds of all broiler chicks produced are crossbred, while 70% or more of all breeding flocks in the United States are either hybrids or crossbreds. It is impossible to tell now whether the same amount of effort expended in the improvement of large closed flock populations by selection would have produced better or poorer results, but the exceedingly skilful exploitation of the hybridisation techniques by their early developers has forced most surviving breeders of poultry for competitive reasons to apply the same methods.

All of these factors have been influenced by and contributed to the fourth one, the increased size and drastically decreased numbers of breeding establishments Apart from the simple fact that the successful firm ordinarily expands at the expense of its less fortunate competitors,

a critical mass is needed in order to obtain a certain rate of improvement. Only a large enterprise can sustain widespread advertising and permit the breeder to develop the expensive inbred lines and to employ professional planners and managers. Air transport of chicks and the franchise system have made this possible. Lerner (1962) noted that some thirty-five years ago in the Province of British Columbia with a total human population of under three quarters of a million there were more than one hundred breeders of egg-laying stock. This is to be contrasted with the twenty-nine members in 1962 of the Poultry Breeders of America, which is the association covering both the United States and Canada and includes not only breeders of egg-laying stock but also chicken meat and turkey breeders. It may be added that the 1963 membership roster of the same organisation was reduced by some 10% to a total membership of twenty-six. Because of the high capital investment which is now required to enter competition in this field, it seems unlikely that the number of independent breeders will ever increase.

There is probably no future for a company which is not big enough to support the research and development to maintain its position. The application of genetics and the results of laying trials have reduced the breeds and strains to a very small number. The laying birds now available are all very similar, so that success or failure of a business will depend, in part, on how efficient the breeding system is for making further gains, but increasingly on the sales organisation.

Having forced out the small breeder, the few remaining large establishments are now engaged in competition with each other, and are beginning to depend more heavily on foreign markets to maintain their financial soundness. The picture in many ways is very similar to that of the motor car industry in the United States in which only four companies are now left out of the hundreds that came into being since the time the automobile was invented, and in which one corporation produces more than half of all the cars made. There is a further analogy with the motor industry. Just as both Ford and General Motors had to diversify their products and put out cars, trucks and tractors, so do the breeders of one kind of poultry apparently need to expand by breeding other types of stock. Thus many of the breeders of egg-laying stock are also attempting the improvement of turkeys and some participate in the broiler industry. Indeed, in some ways, Great Britain has already outpaced the United States: at least one poultry breeder has entered both the sheep and the pig industries.

That there is an opposition to the trend from many sources is undeniable. Truths, many half-truths and a variety of myths (some

examined by Robertson, 1964) about allegedly anti-humanitarian aspects of modern agriculture complicate the issues. The opinion is often expressed that the intensively produced foodstuffs are tasteless. Whether this is the case or not remains to be demonstrated by objective tests which are now very difficult or impossible to devise. Rapid growth and early killing probably do result in more tender but less tasty products. But the uniformity and reliability of quality in such products as pigs or broilers or eggs has been clearly improved under the intensive system, and from the standpoint of the welfare of society at large there is very little doubt that the increase in efficiency of production of these commodities is a desirable accomplishment. It may also be true that certain types of foodstuffs have become uneconomical to produce and, because of that, scarce. Thus, the roasting fowl has practically disappeared from most American markets. Similarly, should a consumer have a predilection for dark brown eggs, he would be hard pressed to find them at the ordinary grocery counter in California, because compulsory candling is now done by electronic scanners which cannot detect bloodspots in such eggs.

It is fair to say that this situation is a reflection of the small demand for such speciality products. Undoubtedly they could be produced and marketed, as they are in Britain, should enough people be willing and able to pay for them after they have become a luxury. To say that brown eggs should be available to all who want them now may be the same as saying that grouse and lobster should be available to all. The fact that at one time such eggs were a common enough commodity is not particularly relevant. Patterns of supply and demand change. Not long ago liver was fed only to pets and was available at very little cost. Today calf liver is not a cheap meat. Turkeys at one time were only festive fare. Today they are often one of the cheapest animal proteins available in accepted form.

IV. The Consequences of Artificial Insemination

Artificial insemination has been both a result and a cause of the revolution in large animal breeding. Its development was made possible, in the face of much criticism, by the efforts of scientists spurred on by wartime shortages and given their opportunity firstly by research administrators and then by dairy farmers. Many experts found it necessary to oppose its use for reasons they will now prefer not to recall, such as the notion that artificial insemination leads to the production of monstrosities and degeneration, inbreeding and reduced fertility. "Unnatural" the process certainly remains, but it proved itself so

economical, effective and advantageous to so many herd owners that it became firmly established in all countries with advanced dairying. For general discussions of techniques and application, Perry (1960), Salisbury and Van Demark (1961) and Maule (1962) can be consulted.

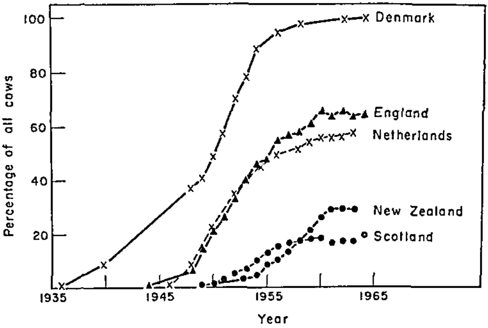
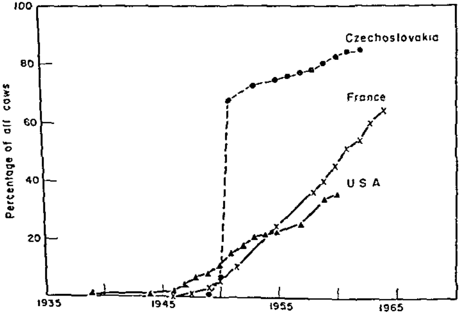


Fig. 6.2. Growth of artificial insemination of cattle in five countries.

The numbers of cows inseminated have expanded in a typical S-shaped growth curve (Fig. 6.2 shows some examples) but there are some interesting exceptions, for instance, Czechoslovakia, United States and France (Fig. 6.3). For these, it may be speculated that the usual growth process is incomplete or obscured by political and other considerations. Where countries have differed is in the point where the rate of growth has fallen away to a low value. The approximate percentages of all cows artificially inseminated in a few countries with large dairy industries are shown in Table 6.1. These few are sufficient to show the wide range of average herd sizes and their relationship to usage of artificial insemination. Distributions of herd sizes would be more informative. In the United States with its diversity of conditions for dairying, a national average herd size is of little informational value.

services are closely integrated, has replaced natural mating almost entirely by artificial breeding. The point is not without significance, since the power of artificial insemination to realise its potential depends on its scale and its independence. Both are likely to be adversely affected by the trend towards better health control and larger herd size through the strength these give to the market for bulls for natural service. Influences working in the opposite direction can be found in the demand for rapid changes in breeding policy especially towards or away from beef production, and in the growing confidence of dairymen in the power of the A.I. organisation to find the improving bulls.



received for those that are still produced must be affected by the cost of the alternative to natural service. Furthermore, when the number of herdbook registrations declines, financial stringency for a breed society follows.

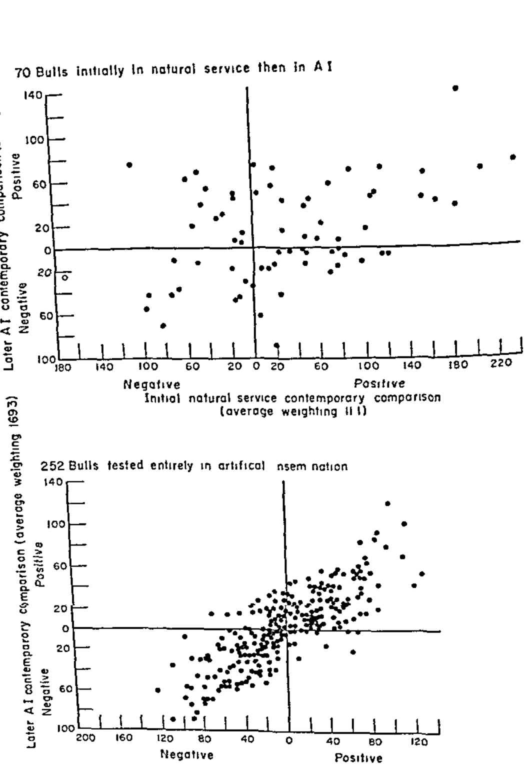
TABLE 6.1

Percentage of all cows artificially inseminated (from Adler, 1964, and other sources)

	%	Average herd size (all herds)
Denmark	100	12
Holland	60	13†
Sweden	30	11
New Zealand	31‡	70
U.S.A.	30	—
England and Wales	66§	24
Scotland	19§	44

† Tested herds only.
‡ From James (personal communication, 1965).
§ From Melrose (in Maule, 1962).

Artificial insemination has also brought powerful influences to bear in other ways. Farmers are now able to change their breed by grading up and to switch from dairy to beef-type calves very quickly. This resource in farmers' hands can lead to chasing the market and thereby cause over- or under-production of both types. Another result is to bring rapid changes in breed numbers. For instance, only 36% of Ayrshire cows in England in 1963 were bred to Ayrshire bulls. Of the rest, one-third were inseminated by Friesian semen and two-thirds by beef semen. A change in popularity can be given expression much more promptly than formerly.


70 Bulls initially in natural service then in A I
Later A I contemporary comparison (average weighting 156 8)
Positive
Negative
140
100
60
20
0
20
60
100
180
140
100
60
20
0
20
60
100
140
180
220
Negative
Positive
Initial natural service contemporary comparison
(average weighting 11 1)
252 Bulls tested entirely in artifical nsem nation
Later A I contemporary comparison (average weighting 169 3)
Positive
Negative
140
100
60
20
0
20
60
100
200
160
120
80
40
0
40
80
120
Negative
Positive

on test. The figure embodies the advances made in physiology, genetics and data handling, which are adopted in different parts of the world with varying degrees of collaboration from breed societies. While such collaboration is helpful, it cannot be regarded as essential. The organisation which possesses the information on performance and has the staff capable of analysing it, is in a strong position. Indeed the emergence of a body of people with statistical machinery at their command and with the means of publicising their studies and conclusions has altered the status of the private breeder substantially. It is not surprising that sometimes he wishes to retain the importance of eye judgment and the value of winning show classes on visual appraisal, but he has now to contend with the fact that the economic characteristics are recorded and interpreted by scientists. One of the first things these people did was to reveal that genetic differences between herds were very small. In so doing, they undermined the foundations of pedigree breeding (Pirchner and Lush, 1959).

By virtue of their scientific and field staffs and central data processing, A.I. organisations are capable of carrying out operational research of value to dairymen. Witness to this is given by the annual reports of the New Zealand Dairy Production and Marketing Board and the Milk Marketing Board of England and Wales. The same publications are also stimulating to research workers and point the way to closer contact between research institutes and A.I. organisations which would benefit both parties. Indeed, as the collaboration at Cornell and Edinburgh of research workers and A.I. centres has shown, the fruit may be enjoyed over the whole world. It also suggests a means by which modern constructive breeders and those adventurous spirits who always are willing to try something new can obtain the use of up-to-date techniques and skills.

The pioneer work carried out with dairy cattle will be available to guide and hasten the development of artificial insemination with pigs, as the physiological limitations are overcome. In the U.S.S.R. the use of artificial insemination in sheep is already more extensive than in cattle. Pigs and sheep have yet to go through the stages of searching for and finding animals of superior performance to use in artificial insemination. There seems no reason to doubt that such animals exist but the finding of them will require arrangements at least as refined as those applying to dairy cattle. It can be anticipated also that the controversy between the proponents of type and the proponents of performance in terms of growth rate and fertility and other quantitative characters, will be revived. As evidence accumulates, it seems, however, unlikely that any pursuit of type for type's sake will last much longer.

Where type has a proven relationship to economic output, it will, no doubt, be retained as a criterion of selection.

The technique of deep freezing of semen makes it possible in theory to test long-dead ancestral sires against their modern descendants (see section on gamete preservation in Chapter 8). Whether any animal breeding institution would be willing to embark on long term deep freezing of sufficient semen in sufficient variety and then test it, remains to be seen. It would run the risk that ideas on conformation and on the proper objectives for breeding have so altered that no farmer would willingly agree to the use of the semen on his animals. Furthermore, there might be some uncertainty as to whether any gametic selection had taken place during the long freezing.

V. Improvement through Artificial Insemination

That there is scope for improving methods of selection among dairy sires is shown in an analysis by the United States Department of Agriculture (1964) of 1046 A.I. sires and 1508 naturally mated sires. Seven breeds were studied. Of the A.I. sires, only 46% maintained or increased milk yield and, of the others, only 51% did so. To estimate the amount by which yields of dairy cows have been raised by artificial insemination has so far proved a rather intractable problem. No doubt the merit of commercial cattle has been raised by progeny testing and preferential use of the superior sires, but there are few firm calculations to show by how much. For discussion of this problem, Robertson (1960a), New Zealand Dairy Board (1961) and Van Vleck and Henderson (1961) should be read. Table 6.2 has been extracted from more detailed information in a recent report of the New Zealand Dairy Production and Marketing Board (1964). Although only a minor fraction of the national herd is as yet bred from A.I. bulls (including young ones being tested), the calculated increase in earnings, if realised, would be substantial and well worth having in addition to the other useful services provided The monetary cost of securing these earnings will be of great interest. At 3 shillings a pound for butterfat, the increased production of artificially bred cows is at present worth to a New Zealand dairy farmer about 60 shillings ($8.40) in each lactation.

Outlays on recording yields and testing bulls are in part an investment in the breeding of more profitable animals. To decide how large that part is, will probably engage economists for some time, but the effort should be made Poutous and Vissac (1962) have made a start by considering the progeny test of bulls used for artificial insemination as a financial operation on behalf of the members of a centre. Profitability

TABLE 6.2

Estimated increases in numbers of artificially bred cows and sales of butterfat from a population of about two million dairy cows in New Zealand (from New Zealand Dairy Production and Marketing Board, 1964)

Year	No. of 2-yr old cows in milk bred by A.I. (in thousands)	Superiority of A.I. stock (lb fat)	Increase in earnings (in thousands of £)
1952–53	0 4	+10	0·6
1957–58	21 0	+15	81
1961–62	81·0	+19	584
1962–63	103·8	+20	822
1963–64	124·0	+20	1056
1966–67	147·3	+25	2093

will be affected by the purchase and maintenance costs of bulls, the amount of semen sold, the cost of collecting the data, and the benefit of the extended use of the best of them. Upon the answer depends a rational decision about the amount of money that should be devoted to this activity. It is not necessary to wait for the answer, however, before deciding that a breeding programme designed to maintain a balance of opposed objectives (such as more meat and more milk from a cow of fixed size) will not pay dividends on the investment.

So far, A.I. operators appear to have acted on their own or their customer's faith in the ultimate returns on outlays for improvement. Until they set out their breeding aims and show that their expenditures on performance testing are consistent with these aims and economically justifiable, there is no way of deciding whether such work should be expanded or contracted. By degrees the logic of events is pressing them slowly towards a decision on breeding aims. Unless each generation of bulls for artificial insemination is the product of the previous generation on which money has been spent, the profit from all the work on improvement through breeding is limited to expanding the use of good bulls in commercial herds and reducing the use of poor bulls. Rate and direction of change are still influenced by the breeders from whom A.I. bulls are bought. In a large business for which cattle are only a means to making money, the question "does it pay" has to be answered for the whole concern. It is directed to the kind of cow to be bred, to the policy of pure breeding, and to the amounts invested in improvement. Whether

or not to bother with numerically weak breeds is another unhappy problem.

Where the breed associations are already closely integrated with artificial insemination and other services, as in Sweden and Holland, the conflict of interest is less acute and less apparent than in countries where they are not. In these, it seems that those who control artificial insemination will sooner or later be forced for economic reasons to use its potential to breed the kind of cattle customers want as fast as possible. They are not likely to do this until they have secured the support of dairymen, technical staff and equipment, and courageous leaders. If they reach this point they will feel strong enough to settle the issue about breeding objectives and if necessary act independently of the breed associations. The latter, however, are likely in this event to modify their ideas, rather than lose the market, as well as the technical help that artificial insemination can give. When this happens, the way will be clear to follow one or more jointly pursued breeding policies with new stratifications of animals and men based on new definitions of performance. Only then can the combined strength of the A.I. organisations and the breeders be brought to bear on (a) efficient purebred selection, (b) the production of distinct breeding lines within breeds, (c) developing cross-breeding merit, and (d) new breeds.

The Danish version for swine (Lush, 1936; Jonsson, 1965) is also large scale in that it applies to the whole of the nation's stock. The concept is of elite herds breeding improved animals with the aid of progeny testing and technical supervision of breed type and performance. Swine breeding is based on 250 accredited breeders. In order to qualify for the title of "accredited", breeders' herds must not only perform to certain standards, both at home and in the testing station, but the breeders themselves are subjected to careful personal and technical selection. Their efforts are coordinated by an integrated system of advisers, four large testing stations, and recognised breeding centres or farms which have a total of about 3000 sows and 700 approved boars. The advisory service is run by Farmers' Unions.

Since the Danish bacon industry is highly dependent on an export trade which is very selective in its requirements, it is essential that the aims of breeding should be carefully aligned with the requirements of the export market and that the aims should be faithfully pursued by all the accredited breeders. Under such a system, the advisers should be well-informed, their statistics should be up-to-date, their interpretations of them should be correct, and prices should be favourable to official policy.

So far, this system seems to have worked well, at least in the absence of equally well organised competition. Naturally, there are problems and, naturally, the statistics also tend to be out of date when they become available. A task of the decision makers is to recognise deficiencies before they become serious and to take the right corrective measures. At the present time it appears that the success of the Danes in increasing growth rate and meatiness has brought a problem with it. There is evidence that some of their swine are becoming genetically liable to show a pale and watery flesh after slaughter, but there is also central authority able to direct research to the difficulty, and to see that the solution is promptly applied.

Although Danish swine breeding approaches large scale breeding in the sense used here, it does not fully qualify, because decision making in regard to breeding, although limited, is still in the hands of the individual accredited breeder.

A large scale breeding enterprise differs in one or more respects from this and other examples of the pedigree system:

1. breeding is a means to efficient production (and is not an end in itself);
2. breeding is based on modern scientific techniques;
3. breeding is closely integrated with centralised financial, managerial and marketing control.

A large scale breeding enterprise is not primarily concerned with breeding but with production and marketing. As the beef lots of California show, some relatively large businesses produce animal products without an integral breeding scheme. Where varieties of livestock of superior merit are bred for the purpose in hand, it is necessary to have sufficient resources to finance the project. These usually come from current profits on production and sale, so that there is a direct connection between the end-product and the amounts expended on research and development. For the most profitable use of these funds, breeding must be carried out on an adequate (but no greater) scale, have clear-cut aims, and apply the most effective techniques.

From the purely genetic point of view, the advantages of large scale breeding do not follow automatically from large numbers. Artificial insemination of dairy cows, for instance, is usually an extensive operation in terms of numbers of cows inseminated but it has often been conducted with no serious attempts to breed improved cows. Because it will pay for itself without doing this, because operators are often not subject to competition, and because opposition is raised by breed associations, some of the essential features of the poultry breeding revolution are missing. In Western Germany, France, and Holland the organisation of artificial insemination is much sub-divided so that the individual centres tend to be relatively small and have neither the scientific staff nor the cow numbers to mount long-term breeding programmes based on sire testing.

compete in terms of total mixed purchases instead of specific items (hence "loss-leaders"). Both can be turned to advantage by vertical integration because the several steps in production and marketing can be coordinated. The hazards of over-production by enterprises seeking cost efficiency through large scale production, look as if they are being countered by forward contracting for supplies of fixed quantity and quality. Adapting breeding stock to meet the requirements is therefore becoming more urgent.

How far the combination of finance, husbandry and breeding skills, ease of transport and storage, and uniform consumer demand, that set the stage for the events in the poultry industry, can be matched with large livestock remains to be seen. It could happen, as in the past, that some of the economic or productive advantages of large units will be sacrificed in order to gain political and social ends. If this does happen, it will not necessarily happen to all kinds of activity. Small co-operatives although begun by groups of comparatively small scale farmers for buying, selling, or operating artificial insemination services, may turn out to be more of a burden than their founders hoped. Without sufficient scale, they cannot reap the advantages they seek and they may often be glad enough to throw in their lots with larger enterprises.

The present methods of breeding chickens are financed out of the profits flowing from the conjunction of large numbers, advanced technique, and unified direction. All these components are necessary for the rapid production of improved breeding lines, for extensive trials, as well as for the exploitation of the answers on an industrial scale. As far as artificially inseminated dairy cows are concerned, all are present in the U.K. and U.S.A. except the unified direction. Beef cattle are not poised in quite such an advanced position but are rapidly approaching it in the U.S. on three fronts. Artificial insemination techniques are being adapted to the circumstances of beef cattle, and organisers now have the great advantage of being able to obtain performance-tested sires. When these two techniques are allied to those of intensive dry-lot feeding, all the conditions for large scale breeding enterprises could be met.

Swine production seems in some ways ripe for development along these lines. Intensive husbandry offers scope for technical expertise in breeding and marketing, but organising it on a sufficiently large scale without the help of artificial insemination has still to be accomplished. Artificial insemination is of course possible with swine, but as yet hardly economic, except where large populations of sows are already concentrated.

In spite of its popularity in the U.S.S.R. and Eastern Europe, artificial insemination of sheep has not yet found itself a useful purpose elsewhere. Nor is it likely to, while the aims of breeding are ill-defined and the methods by which superior sires might be found are ignored. As with swine, therefore, the building up of large breeding units must be founded on something else. Many flocks quite large enough numerically to support a scientific breeding programme already exist but are not doing so. A few of the reasons can be imagined. Sometimes the profits are too small to support developmental costs; sometimes they are too large to stimulate ambition. These reasons always exist. Additionally, however, the prospects of breeding and exploiting superior sheep for an extensive husbandry (under which the large flocks tend to be kept) are not as attractive for the time being as they are for intensively managed flocks. For the latter, there would appear to be opportunities for raising output substantially by applying new technical knowledge in husbandry and breeding.

The paths towards the integration of breeding operations, as a comparison of the U.S. with Denmark shows, are not a simple function of the size of a country or its form of government. Pigs and dairy cows are bred in Denmark towards economic objectives within a form of co-ordination quite unlike the system which has evolved in the U.S. for poultry. Furthermore the paths are not mutually exclusive, either within an industry or between industries within countries. In practice an established system can present obstacles for any other. The public financing of teaching and research committed to the pedigree system, subsidies for performance testing, and official attitudes about breeding can hinder, if not prevent, new and possibly more effective organisations from arising.

Alongside the poultry industry, there exist both in the U.S. and in the U.K. co-operative ventures in dairy cattle breeding designed to overcome the disadvantages of relatively small herd size by subjecting the co-operating herds to a single breeding plan. With the aid of deep-frozen semen and artificial insemination, a group of institutional herds mustering some 700 cows in North Carolina and centred on the State College at Raleigh has adopted a concerted policy of testing young sires and exploiting the best. Semen is available from four proven sires. These are selected from an intake of three or four recruits each year which are laid off after test matings in a young sire proving programme.

A similar scheme has been organised in England around the Cambridge A.I. centre. This one involves about 2000 cows in co-operating herds and has a similar breeding plan. In both countries private breeders are learning to combine to achieve more suitable numbers for giving

effect to their own ideas of type. It must be left to the future to show whether these groups can be held together. Some at least are likely to dissolve on account of dispersals, retirements, and disagreements. In Denmark, the process of co-operative breeding has been carried to the logical end point, where practically all breeding is based on local A.I. centres guided by results from the progeny testing stations.

Inefficiency of selective breeding in all its versions is paid for eventually by the nation, but more immediately by commercial producers and processors. The direct beneficiaries are a small proportion of all pedigree breeders, and those who are employed by them. Whether the maintenance of the pedigree system is a satisfactory protection against real or imaginary anti-social consequences of large scale businesses must depend on the rate at which it can evolve into a more efficient system. In its present diffuse form it cannot attract either the capital or the highly skilled, scarce and expensive organisation men capable of exploiting both scientists and salesmen.

VII. Contract Farming

Smooth flow is important in keeping costs down for the packer who prepares foods for an exacting retail market. Supplies by small farmers are too irregular, and, hence, they must combine to obtain contracts. A great variety of contracts is being tried out. Much depends on who is to do the risk taking: a banker, feed merchant, hatcheryman or final producer. Contracts increasingly specify the breeding, dates of delivery, and quality standards. The planning and discipline required are offensive to some producers.

In the United States broiler industry, a producer usually does not buy the stock or the food for it. Some contracting company will pay for all this, supervise his operations, and pay him a flat rate to cover his labour costs and depreciation. If there is a profit the company will share it with him. Depending on the contract, he may also share any losses.

Contract farming is not incompatible with good stockmanship. In fact, the converse is true. The poor stockman and manager is unreliable and an unsatisfactory partner for a contract. Efficient producers, however, acquire a powerful ally to help them with capital and technique and they stand to gain from integration.

In an industry as diverse as livestock production, it is not helpful to think of either the horizontal integration of small enterprises engaged in the same activity, or the vertical integration of adjacent stages in the process of production as if they were exclusive and unable to co-exist along with traditional farming organisation. Contract farming is a

response to economic pressures and will grow where these are strong enough. Just as it may replace existing arrangements or add to them, so may it invade old markets or develop new ones. It may appeal to some farmers while repelling others who would sooner accept lower returns than be bound. So far, opportunities for contract farming seem to be greatest where intensive controlled-environment production means comparative freedom from fluctuation in supply due to weather, and easy access to retail markets.

VIII. Growth of Big Business

A reduction for all to see is now taking place in the number of independent breeders of most species of animals, and with it a strong tendency towards integrating all phases including, breeding, feed supply, equipment manufacture, medication, operation of a producer's plant, and processing as well as merchandising. Furthermore, this process of integration, at least in the poultry industry, is evolving on an international level. Production of both broiler and layer stock in Western countries is controlled by relatively few companies interlocked financially or affiliated in other ways with companies in other countries and continents. It may be a long time, if it happens at all, before a single giant company attains a monopoly and thus stifles the rivalry of which the consumer is a beneficiary. A decline in the number of independent firms controlling production of all food of animal origin could lead to reduced competition between different kinds of meat for the consumer's favour which keeps down the price he now pays for the product of his choice.

The rate of increase in the size of businesses, however, shows much variation. The largest firms in each industry with their supposedly superior efficiency do not always overwhelm their rivals completely, and incidentally gain whatever advantages there may be in having a monopoly (Florence, 1964) Some of the differentiation of industries lies in their distribution For one thing, they may have to be near their raw material For another, the degree of uniformity of the product and the conditions of demand will affect output. In communist countries demand is made uniform and, therefore, the advantages of large-scale in manufacture are achieved but these are denied where customers insist on a lot of variation. The less uniform the conditions of supply, the smaller the plant or firm tends to be. The outstanding examples are to be found in types of farming subject to the behaviour of weather, so that the performance of livestock is not reliable. If both farm enterprises and retailers are small scale, large wholesalers will usually be

interposed between them. The size of an organisation may also be related to the ability of its employees to run it. This, no doubt, applies not only to farms but to public corporations and even governments.

Arguments both for and against the monopolistic trend which may be developing can be made. The good comes from the production of better stock faster and more efficiently while there still exists competition between the growing giants of the industry. The bad comes from the eventual control of a sector of agriculture by a few individuals whose interests may not correspond with those of the public. Whatever the case may be in manufacturing industries or in agricultural production, in animal breeding monopoly could lead to a biologically irreversible state. The capital investment required for establishing a new breed, a new artificial insemination service, or a new source of supply of breeding stock for multipliers and hatcheries, becomes incommensurate with the risks and expected returns when an established monopoly is being challenged Spontaneously arising competition with breed monopolies is not to be expected. The break-up of trusts by government action may not be helpful if in the meantime stocks are reduced to a single and relatively homogeneous gene pool (or single sources when at least two are needed for crossbred production). Some loss of genetic variation is implicit in progress by breeding, but a further loss due to trimming the costs of maintaining unrelated stocks in a monolithic organisation might mean reduced adaptability. Fear of this, however, may be misplaced and, in any case, is not a sufficient reason to insist on retaining outmoded methods of selection.

A successful organisation, successful in the sense of having survived and grown, tends to become committed to policies based on ideas that have proved sound in the past. No reason suggests itself for exempting business firms, breed associations, dairy boards or government agencies from this generalisation. Largeness tends to encourage qualities of maturity, a desire for stability, avoidance of risks, a tendency to lapse into routine (De Carlo in Ginzberg, 1964). Too much of this kind of commitment may cause an enterprise or industry to miss opportunities for applying new methods through fear of the risks of deviating too far from past practices. For the managers of the large organisations there is a problem of adaptation to face. To add to their troubles in assessing scientists, systems experts and accountants, as well as the welter of incoming data, there is the duty to design new relationships between people within enterprises instead of new products themselves. For broader responsibilities of this kind, men are needed who will not retreat into technicalities of a lower order (for references to books on the developing management science, see Wearne, 1965).

There may be a danger that the emerging giant enterprises of animal breeding will suppress all other smaller forms of business, by being more efficient and competitive, and then relapse into stagnation. Perhaps there is a new kind of establishment growing up with great promise but in truth destined to become intolerant of domestic critics and independent reformers alike. Such fears may be ill-founded or concern only a distant future, but it may pay to devise some means of discouraging complacency or reaction in the management of the powerful new devices for breeding livestock.

The arguments in favour of bigness apply to larger animals as well as to poultry, but, as already pointed out, it does not follow that the re-organisation which has taken place in that industry will be the exact pattern for other industries. The size and capital value of a single animal, its adaptedness to intensive management or automation, its susceptibility to precise grading and contract deliveries, all will affect the size and design of production units. Stock other than swine and poultry, that is, stock more closely dependent on the kind of land they occupy, will provide opportunities for units varying widely in size. Some co-operative ventures are based on specific and limited aspects of farming, such as syndicated groups buying calves or young pigs. These kind of activities, which imply no large outlays on offices and administration and do not tax the skills of the farmers running them, may be all the bigness that some circumstances will support.

Although the tendency to increase the size of the productive unit has been shown in all industries including livestock production, it is still uncertain how far small businesses are doomed to be swallowed up by big ones. In agriculture, individual enterprises are relatively small (although growing in size). Somewhere in the whole process of production of which farms are a part, bigness may be necessary. Necessary or not, it is a fact already in many aspects such as the slaughtering, shipping, and storing of meat, manufacture of fertilizers, herbicides and pesticides, and artificial insemination. Florence (1964) interprets this trend towards large scale operations as a result of the law of increasing return. An increase of capital and labour generally tends to create an improved organisation which raises the efficiency of capital and labour.

As breeding becomes industrialised, it is increasingly subject to considerations that are quite foreign to those who practice the traditional art. In this context it is worth pondering Korach's four laws of technology (in Goldsmith and Mackay, 1964), since much of what is happening may stem from them:

1. The law of the cost variable: each process has a maximum allowable cost determined by the market price of the product.

2. The law of the great number of variables: in technology only a limited number of variables, the dominating ones, can be considered.

3. The law of the scale effect: at a certain degree of quantitative change, a qualitative change becomes necessary.

4. The law of automatisation: the range of variability can be held between determined limits only in automatic processes.

CHAPTER 7

BREED ASSOCIATIONS

The conscious creation of breeds of livestock is a comparatively recent development. As breeds go, Corriedale and Columbia among the sheep, Santa Gertrudis cattle and Lacombe pigs have a well-documented but brief history. By comparison, the origins of the Shorthorn, Hereford, Friesian, and the Merino recede vaguely into the distant past. Local varieties that were to provide the basic material for the breeds that established themselves in the nineteenth century must have been numerous, unstable, subject to war and pestilence, and crossed with the cattle of traders on stock routes. Blood group studies, like the morphological studies before them will, no doubt, endeavour to trace migrations and relationships amongst breeds, but it is uncertain whether they will ever succeed in unravelling the tangled skein.

It seems (Lush, 1945) that a likely sequence of events in the history of a breed would start with relatively high market values for some local variety and continue towards meeting a demand for pedigrees. This would narrow the sources of supply and maintain values. By no means all local varieties got that far. In his book on pigs, Davidson (1953) mentions twenty-two of them in England alone that failed to attain

breed status. Shorthorn cattle, in contrast, became popular, which led to the compilation of the first cattle herdbook by George Coates in 1822. Export markets often stimulated formal breed establishment. Later, the influence of shows made it worthwhile to follow fashions with respect to type. The formation of breed societies in due course (to produce the herdbook and to promote the interests of breeders) brought about the emergence of men who were confident in their judgments and opinions. It led them to make assertions about correct type, and to explain why it was the correct type. For many breeds, export markets were very important in fixing breeding aims. Just how far demand from overseas was itself conditioned by notions of type obtaining in the home market would now be difficult to find out. Ideas about correct conformation, colour and quality of coat were very likely shared, though the reasoning behind them might have been quite wrong both at home and abroad.

I. What Is a Breed?

A population of farm animals is a breed, for practical purposes, (a) when it has some identifying features, or (b) when it has a formal association of breeders, or (c) when certain government officials say it is. These definitions are clearly not independent of each other, but they have nothing to do with performance, local adaptation, market demand or fertility, in spite of the fact that existing breeds are often described in such terms. In their early stages they all have a geographical focus that made it possible for breeders to develop joint breeding and selling policies. Although not so obvious during the growth phase of a pedigree population, the focus can usually be located by the concentration of long-established flocks and herds and, in bad times, by the shrinkage towards it of the area colonised.

is a stratification in each case which encourages matings within the limits of adjacent strata without actually prohibiting them outside those limits. The net effect is a force generated by the attractions of the elite class, and holding a breed together. This class is to be thought of as an amalgam of 10–20 breeders with their associated stockmen and their animals.

Other forces superior to this one and centrifugal in character can develop within a breed. Inside a breed association, disagreement about type, and, therefore, about the main purpose of the breed, may arise and become the first stage in a new definition of breed standards. The population then may split into two or more sub-groups. This is likely to happen to a breed that is widespread, so that local varities appear within it and develop a cohesion of their own. The sub-division of Shorthorn, Jersey, and Dutch Friesian cattle are well known examples of this process.

It has often been urged (in fact, since Culley, 1794) that there are too many breeds, a view provoking the question: too many breeds for what? The numerically weak ones make no perceptible difference to the economics of farming or to the range of products. The owners may be animated by sentiment rather than by economics, but their sentiments could be tolerated by the majority with good grace. An improvement of 1% in the economic merit of Suffolk or Hampshire sires of crossbred lambs would increase quality or production more than eliminating a few relic sheep breeds. Some commentators seem to overlook the point that countries with a wide range of environments for livestock cannot escape from a substantial amount of variation in market products simply by weeding out a few unimportant breeds or crosses. Much of the variation in the size and shape and fatness of carcass meat comes from environmental causes, and much of that from within farm and breed.

The main practical guides to a breed are the breed points which are specific details of colour or conformation mostly of minor economic importance. They have come in for much criticism but there is something to be said for them. Advocates of functional beauty may be underrating the importance of breed points like colour. They confer the uniformity and the trade marks by which breeds can be easily recognised. It is, after all, a very human characteristic to be attracted by appearances, and it is likely that, so long as the users and raisers of the larger farm animals are very numerous, there will, for a long time, be a market which is influenced in favour of attractively produced animals. No doubt functional beauty will gradually count for more, and no doubt production and breeding will fall entirely into the hands of those who

rate performance higher than appearance. But in the meantime, there is some way to go before breed points, in all but poultry, cease to be of significance.

II. Breed Purity

Pedigree breeders usually set considerable store by breed purity, of which the visible manifestation is an accurate register of pedigrees. Yet the value of an unblemished pedigree for export purposes is problematical and is, in any case, of little interest to the great majority of livestock farmers. There is no means of knowing now how often gene migration occurred in the past from breed to breed by accident or surreptitious crossing. Some breeds may be more important in maintaining heterosis in other "pure" breeds than is recognised. Indeed, early pedigree breeders often kept two breeds.

Two reasons suggest themselves for trying to isolate breeding populations and prevent migration of genes. Firstly, a breeder may wish to maintain genetic identity by avoiding mixing with other stocks. This applies particularly to inbred lines, novelties, or highly selected lines which would be much reduced in value by dilution or by rising too rapidly in numbers. Secondly, there may be a commercial value in the mere idea of purebred, or "well-bred" animals or in the stock of particular breeders.

Neither of these reasons has much genetic validity in a long established pedigree population, barely distinguishable in performance from common stock. The latter, in fact, if bred by successful artificial insemination sires, may be superior in some respects. Making it easy for such animals to have descendants eligible for registration in open herd books would seem to be sensible. Practice in this matter varies among breed associations. Those which insist on unsullied pedigrees may be doing themselves harm. In addition to the expense of keeping and checking the necessary records of acceptable animals, registration fees from those which are unacceptable are lost, and some possibly useful genetic variation and plasticity excluded. Since sales of breeding stock are determined mainly by the breeder's name and, to a growing extent, by performance records, rigid maintenance of breed purity could be unprofitable. With a more liberal attitude to grading-up, based on the finding that animals entering an open herdbook through a grading-up scheme do so at the bottom of the hierarchy, and, therefore, rarely leave descendants in the top herds (Robertson and Asker, 1951, Wiener, 1957), breed societies could enlarge their populations of animals with benefit to themselves. Shortening the time necessary to

achieve full herdbook status, relaxing the standards applied to entrants to the first stage, and reduced fees, might increase the number of interested breeders.

To adopt a more realistic policy, however, in the matter of breed purity is difficult for a thriving association and, probably, ineffective for a declining one. What is required is a change of attitude: less emphasis on hollow claims of animal ancestry and increased emphasis on a progressive outlook among members. As interest in tests of performance grows, it seems possible that unregistered animals which have done well will sometimes become influential in a breed. They may be accepted into top herds like imported animals or they may help to provoke the constant review of breeding objectives.

The time for a breed association to encourage grading-up is when a breed is increasing in popularity. With the aid of the fees and membership dues thus added to the finances, the growth impulse is stimulated and will carry the breed further and faster in numbers than it would otherwise have done. In the past, there may have been less force than there is now to this argument, owing to the greater weight formerly attached to breed purity. The problem for breed associations is to judge where their interest lies. It is a question of timing changes in the rules to suit the economic changes in the market for pedigreed animals.

The rate at which these changes take place varies with country, with the kind of livestock, the attitudes of officials, teachers, and the press, but most important with the progress of artificial insemination and performance testing. Since the logical result of the latter activities is to establish a hierarchy of performance, there is likely to be a loss of customers for the nostrum of pedigree and purity. Purity, however, is too useful a word to be abandoned altogether, and it will probably be appropriated by geneticists for highly selected lines of predictable performance and some degree of inbreeding, which, superficially, is just what breeders meant by it. The essential difference lies in the diverse interpretations of the word "performance". In the new performance hierarchy, the value of an animal will be the greater, the higher it is. Its position will be determined by the performance of itself and its close relatives and not by its owner or its name.

Well-bred animals will need more than long pedigrees. General Lord Haig said in 1925: "Some enthusiasts to-day talk about the probability of the horse becoming extinct and prophesy that the aeroplane, the tank and the motor-car will supersede the horse in future wars. . . . I feel sure that as time goes on you will find just as much use for the horse—the well-bred horse—as you have ever done in the past" (Hart,

1959). On this issue he lacked imagination. Breeders today have less reason than he did to read the future poorly.

III. Type and Conformation

Of the vast literature on this topic only a few papers can be mentioned here In particular, in the writing of this section Lush (1945), Touchberry (1951), Bayley *et al.* (1961), Taylor and Rollins (1963), Smith, King and Gilbert (1962), Johansson (1964), Taylor and Craig (1965), and James Biggar (in personal discussions), have been drawn upon. A useful review of the subject has been made by Nichols and White (1964).

The aims of pedigree breeding are usually based on the concept of breed type. Type is concerned with general appearance in relation to function as, for instance, it is in beef and dairy type cattle. Within a type, there are an infinite number of local differences in shape of legs, udder, head, or hind-quarters. To some extent these differences reflect variation in health and plane of nutrition, since, obviously, animals vary in shape with age and growth rate Because of the fact that most genes influencing the shape of an animal are not local but general in action, the conformation of one part is closely correlated with the conformation of another. Muscular hypertrophy or double muscling, for instance, alters the conformation of all muscular parts, and not just where it may be most obvious (for cattle see Raimondi (1962) and Lauvergne, Vissac, and Perramon (1963), for pigs see Ollivier and Lauvergne (1964). The summation of all these changes constitutes a new type. In what follows therefore type and conformation will be regarded as interchangeable terms

Whilst it is easy to measure many body parts and discover that they are fairly highly heritable and, hence, responsible to selection, type is as yet conveniently assessed only by subjective judgment. Heritability estimates are scarcer for type than for its components, but on the evidence of the rapid divergence of numerically large breeds into subtypes and then into distinctly different types, it may be assumed that type has at least a moderately high heritability

the chances of rearing an attractive animal. It would be interesting to know which men come to be regarded as good judges and what are their qualifications Are they people who come to the right, meaning popular, decisions in rating show animals? In most countries, judges seem to have been drawn principally from the ranks of successful breeders, that is to say, breeders whose stock is bought by other breeders In the United States, they are augmented by animal husbandry professors and extension workers. Attaining success as a breeder tends to make a judge to a slight degree independent of popular opinion and, to that extent, able to try to modify it.

As shows and fairs have been losing influence on breeding, the judges have naturally been losing theirs at the same time They have lost it to those who wield the power of artificial insemination or advertising, and who may be indifferent to some traditional beliefs about conformation. However, it is usually a purpose of breed societies and show societies to commend good husbandry and good health, to attract the interest of townspeople to livestock, and to provide pleasure for country people. Judges are a means to this end which they combine with the task of maintaining and encouraging what they regard as correct external form.

B. Type and production

Breed type may well be based to some extent on characters of no known economic importance except to sellers and buyers of breeding stock, but this exception is enough to secure attention to those characters. Some breeds have, doubtless, been handicapped in this way, for instance by the requirements of colour pattern in Berkshire pigs and Shorthorn cattle. Breed type has long been highly regarded in Ayrshire cattle although this did not prevent Holstein Friesians from expanding in numbers much more rapidly than Ayrshires in Britain, Canada and the United States.

Among sheep there are extreme wool and meat types, such as the Merino and the Southdown which are not notably good milk producers. Any number of breeds with intermediate combinations of meat and milk and wool exist but none of them seems to have solved the problem of producing a large amount of milk at one time and a large amount of meat at another, or of switching from meat to another form of protein, namely wool. This suggests that the output of any product may be, primarily, a function of total body size In addition, there seem to be certain specialisations which are incompatible with each other. From a big sheep like the Lincoln it is possible to have large amounts of meat,

milk and wool, all produced by the same animal. But none of these traits is exceptionally good when the size of the sheep, in comparison to other breeds, is taken into account. It seems to be a general principle that, in all kinds of animals, extremes cannot be bred for without a relative loss of performance in some other respects.

Visually assessed type is apparently of little proven significance within breeds, so far as milk yield, fertility, carcass quality, wool production, or growth rate go. But over the broader spectrum of breeds of a given species, type is predictive of production of, at least, milk or meat in cattle and sheep, and of slaughter weight in pigs. The dangers of adopting dogmatic attitudes about the relation between type and performance are shown by a comparison of Charollais, Herefords and Holstein Friesians. Each of these breeds is an important beef producer but they are obviously dissimilar in type.

Examples that show how conformation can be related to performance are provided by show-type dogs. In some breeds, development of extremes in special traits has been carried to the point at which biological fitness and the health of the animals suffer, as in bulldogs. In agriculturally important animals, selection is not carried to such lengths, although harmful ideas about conformation have sometimes been held. Thus, hot-blooded Poland China pigs, very small teats on Ayrshire cattle, over-large heads and shoulders on Hampshire lambs which caused ewes trouble at parturition, woolly-faced Shropshires, and comprest Herefords were all favoured at one time or another. A further example is provided by the recent trend towards polled cattle which is removing a once popular but often harmful aspect of type.

Ideal conformation as defined by show judges is not necessarily ideal for commercial purposes, although judges may intend it to be. The ideal for commercial purposes is that which helps to maximise profit. Consequently, it has two main components (a) the minimum standards necessary for sustained production, reproduction and health, as in feet, udder, mouth, (b) any features proven necessary to develop economically important traits, such as size, shortness of leg, plumpness of hams, and small heads

Within these restrictions there is scope for much minor variety of form. A striving after refinements leads to increased costs which arise from culling and expensive purchases of breeding stock inconsistent with the aim of maximising profits from commercial stock. In pedigree herds different considerations apply if there is a profitable market for breeding stock of specific conformation. A true but trifling illustration of this is provided by those sheep breeds with "correct" and "incorrect" settings of the ears and horns.

Although it may still pay a breeder to attend more closely to conformation than to various other aspects of performance, either because his selection of breeding animals is more effective for this aspect than for the others or because buyers are willing to pay him for it, in the long run, any unnecessary diversion of effort is a handicap to the breed. Scope for selection is limited and if too much is allotted to details of conformation, more important characters are correspondingly neglected. In discussions of this topic many breeders regard relaxation of selection for type as merely the first step in a consistent series of moves in the "wrong" direction. It is true that in a small breeding population some erratic changes of type might follow suspension of selection pressure for it. But the deviations would not grow and accumulate unless "good" type is inimical to the desired performance, in which case the change might be quite noticeable and beneficial.

C. Genetic aspects

Rice *et al.* (1957) state that "while there is no genetic antagonism between good type and high production, selection for type alone will have little direct influence on production, and conversely selection for production alone will have little direct influence on over-all type rating." This group of experts can call on others, for instance, O'Bleness, Van Vleck and Henderson (1960), Bayley *et al.* (1961) and Mitchell, Corley and Tyler (1961), to support them. A breeder who reads such a statement out of its context, and who did not know what "genetic antagonism" meant could be forgiven for having his doubts about it. He would be thinking of the fact that cattle can range from extreme dairy type to extreme beef type and would not believe that milk production is not influenced by type. This is a good example of the way in which misunderstandings between breeders and geneticists can arise. A resolution of this particular difficulty requires some patience but is possibly worth it since a belief in the importance of type and conformation is deeply rooted in the minds of breeders and the policies of their associations.

The main sources of trouble seem to be semantic. The expressions *genetic antagonism* or *negative genetic correlation*, which mean in the present context that genetic increases in the average milk production of a dairy cattle population would be accompanied by undesirable changes in type, and vice versa, is, like many more technical terms, forced on authors by the need to condense their writing to save space. Worse still, the qualifications to the generalisations made are not always emphasised. Statistical studies on type ratings are made (a) with data collected on culled herds and (b) in pedigree herds that are

trying to achieve a single officially approved type. Consequently the analysis is conducted on the basis of a highly restricted range of types and highly subjective observations (Van Vleck and Albrectsen, 1965) Correlations that are not significant mean only that within the limits of the material, the data and the statistical methods, no credible association between type and performance is found. It does not mean that none exists, or would not be demonstrable in more heterogeneous populations. Within a long-established breed, however, it seems reasonably certain that a breeder would be wise to discount the importance of type differences of a relatively minor character, if he is primarily interested in breeding for more milk. Sometimes, of course, as a seller of breeding stock he is not Then, he would be right to fear that selection for milk exclusively, or nearly so, would lead to variation in type that he might not desire. Nevertheless, whether they know it or not, milk production is far more important financially to most farmers than small variation within the dairy breed type.

Some generalisations on this topic may not be generally acceptable, but nevertheless, useful in helping to clarify it

1. Type and conformation are two words with one meaning. They refer to the shape of an animal relative to its purpose.

2. If the main purpose of a breeder is to give his animals a certain shape, the most effective way of breeding for it is to select parents on the basis of their merits in this respect.

3. There are general and specific genetic controls of type: (a) general, genes affecting skeleton, or muscling or fat; (b) specific, genes affecting heads or udders or legs. The genes affecting specific regions may in truth be general in their action but not yet recognisably so.

4. The general factors cause variation similar in character to that produced by differences in plane of nutrition or by age Selection, however, can exploit them.

5 The components of type are numerous and of varying degrees of heritability They include bone and joint size (Hereford *vs* Angus), appetite (as shown by depth and thrift), mature size, and rate of maturing Consequently, the effect of selecting for type varies with the component and the emphasis placed on it.

6 Within a breed of moderately uniform type, the minor variations in type have very little influence on milk production, longevity, economy of food use, fertility, or carcass quality of an animal or of its offspring

7. Breeding for extreme types is effective as shown by the history of the Shorthorn and Friesian breeds.

much less selection on the test data than is theoretically possible (Smith, 1963), and the same is true in Britain. Just how much dissipation of selection differential is due to a shortage of suitable animals when they are needed, how much to high cost or negligence, and how much to preserving conformation is not known.

Deciding on the proper balance of type and production is not easy for a breeder. Extreme positions carry risks, but there are breeders who appear to believe that type is of overriding importance. Current show standards for yearling beef cattle, for instance, attract the support of breeders though to others they seem to verge on the ridiculous. It has to be conceded, however, that breeders who take risks of supplying the markets of the world with beef bulls must be allowed to use their own judgment of what is the best way of breeding. The time has come, as the growth of the performance registry in the United States shows, when their assertions about merit in beef cattle are being put to the test of economy and rate of gain and carcass quality. Should it be found that they are mistaken, the usual penalties for such mistakes will be demanded, that is a loss of buyers and the favouring of competitive breeds.

The other extreme position (paying no attention at all to conformation) is impossible, since natural selection removes the worst misfits, but it can be closely approached. Those who advocate or practise selection of breeding stock solely on the basis of one or two characters of high economic importance do so. If these characters have no correlation with conformation, the selected animals, as a group, should be of average conformation, but among them will be some rather poor looking specimens. To breeders accustomed to using breeding stock above average in conformation, even average animals will be repugnant. Those who try to keep a strong selection differential for economic characters will have to overcome their desire for "excellent" conformation and be prepared for an immediate, but not progressive, deterioration of their stock in this respect. Fashions in conformation change, however, and what is "good" now may be superseded by a "better" that is more relevant to economic demands or more adapted to parturition. For the new cattle breeds in Australia and United States, containing a proportion of zebu genotype, acceptance of a novel type may become crucial to their success.

not include conformation. All the other traits are objectively recorded and given an importance appropriate to their economic value, heritability, and correlation with other useful characters because chickens have been bred to fit their purpose with an exactness not remotely approached by larger livestock.

A.I. sires with the best proofs in milk or butterfat yield are apt, in the view of the breeders, to be of undesirable type. So far, large breeding organisations have not been consistent in their attitudes to type. In cattle breeding, the controllers of artificial insemination seem unwilling for the most part to declare policies relegating type to a minor role in bull selection. An exception is the American Breeders' Service (Prentice, 1963), which arranges the insemination of one-and-a-half million cattle and which has decided to ignore type classification. In Britain, type is still important and inhibits the full exploitation of the most outstanding sires as judged by milk yields of daughters. And the costly data produced by progeny and performance testing of swine is not yet put to full use (Smith, 1964).

IV. The Natural History of Breed Associations

Livestock Record Associations and Breed Societies are a part of the cultural inheritance of many countries. Their origins and development came in response to needs that were felt, and their activities, like those of many other institutions before them, tend to become habits essential to their continued existence but no longer serving the original purposes.

As in other social groups, conflict is an essential ingredient of an association's existence. Radicals must always do battle with conservatives but they are bound together by acceptance of a history of judgments on method and beliefs, and agreement to serve the needs of the association so that it shall survive.

In an association of breeders with a common interest in a particular breed the status of an individual has two elements: firstly, the rights pertaining to his membership of the group (for example, to register animals), and secondly, competition among members for position in the social order within the group. Partly as a cause and partly as an effect, high rank in this order is associated with extensive social and business contacts, and with privilege in breeding. This stratification, which is so characteristic of human and lower animal societies, evolved because it was an effective means to survival. It combines the advantages of a large group acting in unison with leadership by a few. The role of those lowest in the hierarchy is to contribute to the funds, buy stock from their superiors, resign in periods of depression, and provide

a reservoir of men and animals in case of need. For the highest, in addition to material rewards, there are the rewards of office, the benefits of distinction in breeding, the right to opinions, and the obligation to defend the group. In all this, the objects or the methods of breeding have been irrelevant. The basic urge is to survive and, if possible, to grow. Beyond that there is no group philosophy.

The concept of breed is intentionally restrictive with a view to benefiting the registered owners who make the rules. The concept is restrictive in several respects, not equally applicable to all breeds:

1. discouraging the immigration of genes by overt or covert crossbreeding;
2. spending selection effort on breed points not essential to the main purpose;
3. concentrating selection on a narrow definition of breed type;
4. resisting emphasis on performance data;
5. discouraging the planned obsolescence which is implied by a policy of improvement.

Wilson (in Finlay, 1925) said that "herd books have had little effect on the methods of the stock breeder. . . . But herd and stud books have made unimportant characters important, handicapped breeds with characters they had better have been without, prevented them obtaining characters which would have increased their value, and debarred them from all improvement excepting from within" With the passage of time some of the force has gone from these damaging remarks. Wilson was, however, regarding it as the duty of a breed association to improve, though this was not and is not its primary object.

How much restrictiveness is in the interest of the livestock industry now, is the question. Assuming that breeds (or other isolates) are necessary, some degree of restriction on the immigration of genes is required. How much of it is desirable depends on the function of the breed or strain An inbred strain involved in a crossbreeding routine would be destroyed if it were badly contaminated. An outbred population of purebred animals, by contrast, owes its future to the genetic variability which enables it to progress. Breeders, therefore, with a regard for their own interests, must strike a balance between the risks of becoming out of date by progressing too little and the risks of letting their flocks and herds lose acceptability by moving too fast.

Unless a breeder has a most unlikely amount of capital to invest in the future, he will not breed animals for which there is no current market. Innovations are hard to get started. The same thing is to some extent true of an artificial insemination service. It may have objectives towards which it is working but cannot get too far ahead of those whom

it serves. It is still the case that sires with popular prefixes can be most easily tested, since dairy farmers prefer them to bulls with unknown prefixes. Part of the activities of a large artificial insemination service however, can be devoted to progressive policies for the progressives among its clientele.

The methods of breeders of the larger animals are basically pure-breeding, mass selection, eye judgment, and, as opportunity offers, an assessment of progeny. In the sense intended here, these methods have done service since Varro. Without doubt, a long future is in front of them. The burden of the geneticist's complaint is that they are inefficiently applied, and, inevitably so, within the context of small independent breeding herds.

A. Rights and duties

No rights or duties have been placed on breed associations by legislation requiring them to improve livestock. If they claim responsibility for improvement in the past, by virtue of the skill of a small minority of their members, they must also accept responsibility for failures. Neither, however, can properly be laid on them. Amelioration of livestock is an exceedingly complex process, in which breed societies and associations have played a relatively minor role. What breeders spend, individually or collectively, on attempts to produce a more saleable article, is entirely at their own risk and wish, and entails no obligation on others to meet the cost. Until recently, this statement would have been regarded as contemplating the obvious. A decaying enterprise, however, can be expected to hope that it will be regarded as essential and enabled to operate on a cost plus profit basis. It could be that in due course this argument might be found acceptable in some form. If so, this form might require certain duties to be carried out in return for financial support, and would effectively alter the character of breed associations Their basic function would have to be transformed into a public service.

B. Mental attitudes

Although the seeds of change had been sown long ago, breed societies and livestock registry associations did not have any serious premonitions about their future until artificial insemination began to expand rapidly after the end of the Second World War. They were used to booms and depressions. Breeds competed and varied in popularity, while types within breeds came and went. But breeders did not doubt that they were

an essential and respected element in the livestock industry. If they had heard of genetics, they had also read in their breed journals that its exponents were unpractical people who knew nothing of breeding animals. If they had heard of the performance trials steadily carried out in agricultural experiment stations, they thought them remote from the breeding of pedigree stock.

Considering that there have been and still are many thousands of pedigree breeders in the United States, the United Kingdom and elsewhere, it is surprising at first glance that not one of them has made a significant contribution to knowledge of genetics. Their associations have a history of resistance to scientific advances dating from their establishment. Under pressure they beat a slow retreat marked by milsetones such as milk and litter recording, performance testing and selective registration. No other behaviour should be expected. Members of breed associations are essentially individualists, combining together for mutual advantage, and working collectively only for bare necessities such as herdbooks, advertising and showing, and such other activities as have also become obligatory. They are producers and sellers of livestock, not research workers or evangelists. They are responsive to economic pressures but not to advice or moralising. They are doers rather than thinkers.

Since there are a great many animal geneticists in the world, it is also surprising at first glance that so few of them personally breed high priced livestock. Contrary to assertions that are sometimes made, geneticists have, in fact, bred commercially valuable stock, for instance, the modern chickens, turkeys and broilers, Columbia and Targhee sheep and Lacombe pig. Thousands of show winners have been bred and reared by college professors who were neither farmers nor geneticists. In the West, except possibly for poultry, livestock are not usually provided by universities or governments (Canada excepted) for geneticists to improve. State supported competition tends to be resented by breeders, and freedom to advertise, or buy and sell stock, or hire skilled stockmen is restricted for geneticists. More important, success in showing or selling would signify merely that some geneticists were as capable as some breeders of practising these arts. Such a demonstration would hardly justify the trouble of making it. At the level of an artificial breeding organisation, a dairy board, or a pig industry controlling authority, whole populations of animals become subject to breeding influence, and it is in these circumstances that the geneticist is best able to apply his knowledge.

It is easy to see why breeders are unreceptive to the science of genetics. The business of breeding pedigree stock for sale is not just a

matter of heredity, perhaps not even predominantly so. The devoted grooming, feeding and fitting, the propaganda about pedigrees and wins at fairs and shows, the dramatics of the auction ring, the trivialities of breed characters, and the good company of fellow breeders, constitute a vocation, not a genetic exercise.

The opposition of the breeder untrained in quantitative genetics springs from a variety of causes:

1. Loss of income or status due to the shrinking market for stock without records of performance, or with poor records. It is better from a breeder's point of view for an animal to have no records than records of poor performance.

2. His distrust of paper records, that is, of records on a few traits which serve as bases for judgments instead of visual assessments of whole animals. It is immaterial to him that the top ten % of a large population in, for example, milk yield is nearly *average* in type. He wants to be sure that the particular animal he uses is at least average. Fundamentally, the problem here is one of objectives, not of methods. Breeders still rank type highly as an objective.

3. The importance he ascribes to ancestors and collateral relatives. To the extent that his knowledge of them does duty for missing data he may be right, but he seems at times to over-value them.

4. His difficulty in accepting the concept of heritability when he is assessing individual animals. He is inclined to attribute to heredity what is due to his husbandry.

5. His belief that in judging the breeding value of an animal by eye there is a skill which gives better results than the machinery of genetics. That there is an acquired skill in judging on appearance, and, perhaps, even an inborn capacity for acquiring it, may be conceded. The difficulty is to find the best application for it.

These are all reasonable objections raised by craftsmen overtaken by mass production methods and a computer technology. Occasionally, one of them may succeed in producing the right article when it is wanted, but the chances of his doing so, and of being recognised as having done so, are too slim to justify depending entirely on him and his fellows or on his methods. Given *the same objectives* but more extensive material the computer will be more efficient than the craftsman. As a result of the combination of artificial insemination and milk recording, breeders now have accessible to them much more information about milk and fat yield than ever before. By making an assistant rather than an enemy of the computer, they would become more competitive.

C. Population dynamics

A population of purebred animals, constituting a breed, has a characteristic structure, which is to some extent determined by the nature of the animals, but to a far greater extent by the nature of man himself. Pig numbers fluctuate more than those of cattle because they are cheaper and reproduce more quickly. Breeders of pedigree pigs wax and wane in enthusiasm correspondingly, and the turnover in membership of breed associations is high. Since farmers who decide to become breeders of registered animals vary in age, ability, and resources, there is great variation in the skill of their operations and the experience and scope they bring to them. The structure of the pedigree industry which has evolved is a workable arrangement for integrating this diverse material.

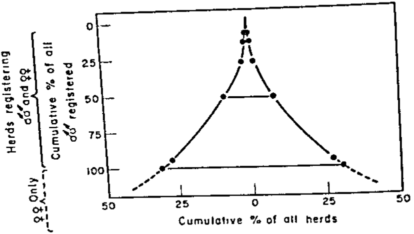


Fig 7.1. Population structure of pedigreed Ayrshire cattle (from Wiener, 1953, reproduced with the permission of *The Journal of Agricultural Science* and the author).

The most obvious feature is the pyramidal stratification of herds illustrated for cattle in Fig 7.1 taken from Wiener (1953). It also applies to other large animals, though in poultry the picture is now different, as has been made clear in the previous chapters. The lower ranks contain what is known as the multipliers' herds and most breeders never rise into the higher echelons Those who do, however, tend to be the ones with older herds of greater than average size. Their output of breeding stock, male and female, increases and more of it finds its way into other pedigree herds. Eventually, a breeder may reach the peak of the pyramid where there are usually ten to twenty herds which are the source of the genetic material that will in time filter downwards. Decisions on breeding policy taken in these few herds will have a predominating influence on their breed, for their herd prefixes will

occur with high frequency in the pedigrees of animals in the lower strata.

It does not matter in fact how the majority of breeders mate or cull their breeding stock, but it does matter how they buy them. They provide the market in which the principal breeders earn much of their income. At the very base of the pyramid are crossbred derivatives of the purebred layer immediately above. It seems more charitable to suppose that those who use pejorative terms like "scrub cattle" and "mongrels" to describe these animals are trying to make debating points than to conclude they do not understand what they are saying. These terms although once valid, are now descriptive of appearance and, since this is mainly determined by the owner's control of disease and nutrition together with his choice of the near ancestry (usually purebred), they ought to be applied, if at all, to his management. Some evidence bearing on the quality of the progeny of allegedly poor specimens has been offered by McLean (1952). Not surprisingly, his reject rams, although scarcely scrub animals, produced groups of fat lambs indistinguishable from those by highly priced rams. Negative measures which are based on discrimination against the "scrub" cattle are not only futile but misconceived. It might well be more difficult to identify the worst genotypes than it is to identify the best if, as is likely, disease is more serious among badly managed than well managed stock.

An hierarchical arrangement is usual where the influence of a few animals is to be made most effective, as for instance in government schemes for breeding and distributing superior stock, or in poultry breeding establishments. In the bull studs of artificial insemination centres it is gradually being developed. Being just an operative technique, there is no assumption that the results are good. It can work to raise or lower standards, and it can work to no effect at all. Although the basic principle is universally applied, there are many versions other than the pedigree systems of the United States and Britain. In Denmark (see Jonsson, 1965, for a clear description) and Israel for instance, breeding is closely integrated with other governmental and agricultural institutions. All systems, however, have the same fundamental distinction between elite and non-elite stocks. Where they differ is in the rules and qualifications of the elite category, and in the form of administration including finance.

To the extent that the elite class is absolutely isolated in a genetic sense, it will undergo a gradual process of inbreeding due in part to the very limited population size, in part to intentional linebreeding or inbreeding, and in part to co-ordinated selection for particular genes. Historical studies (summarised by Lush, 1940) mostly show a rather

slow but persistent degree of inbreeding. Unless, therefore, this is counter-balanced by some outcrossing, a pure breed has this particular handicap inherent in its population structure. The characters which are susceptible to inbreeding degeneration such as milk yield, fertility, and physical vigour, will suffer a decline if enough selection effort in a contrary direction is not exerted. The loss, however, may be hidden by a rising standard of husbandry.

The expectation of life of a registered pedigree herd at its inception is rather short (Donald and El Itriby, 1946). In periods of little or no expansion in population numbers, as many as 50% of all herds started may disappear within five years of their origin. Only a minority at any time will be over ten years old, no matter whether pigs, sheep or cattle are considered. Capital gains, disillusionment, death or retirement take a heavy toll, which is more than matched by the intake of new members in a growing society and which outruns the intake in a weakening one.

Owing to the spread of artificial insemination there has been a considerable reduction in the number of multiplier herds which can find a market for young bulls. This is happening at the same time as the growing power of publicity is leading to increasing importance of the few top men in each breed. Their market for young bulls, both in artificial insemination and amongst the multipliers' herds which remain, is still quite large in most countries (see Fig. 6.2). Consequently, the shape of the pyramid representing the structure of the pedigree industry may be altering. The lower strata of the pyramid may be a little larger than before owing to the number of people who register females only, but the apex of the pyramid may be a little higher (due to the growth in the size of herds) and the waist somewhat slimmer, through the loss of some of the multipliers' herds.

Herd and flock sizes tend to be small, especially in the younger age groups. In Britain about half the registered sheep flocks are of less than fifty ewes (Wiener, 1961). Ayrshire cattle herds, which tend to be comparatively large among dairy breeds, contain, on average, about seventy cows. Most pedigree herds of other breeds will be substantially smaller. By genetic criteria, both the size and the duration of most pedigree flocks and herds are ill-adapted to the task of constructive breeding Selection differentials are inevitably small, progeny testing is restricted and there are too few generations of animals to achieve much.

Bulls used in natural service fail, more often than not, to have ten daughters with recorded milk yields. The risks of making wrong assessments of sires that have few daughters is brought out in Table 7.1. This shows the distribution of sire estimates made by the contemporary comparison method on samples of varying size drawn from 1050

daughters of a bull used for artificial insemination which, on average, exceeded their contemporaries by 23 gallons of milk. With sample sizes of ten daughters the probability of misjudging the sire's genotype by 25 gallons or more either way is about 67%.

TABLE 7.1

Percentage distribution of sire estimates made by contemporary comparison on samples drawn from 1050 daughters of an A I bull with a contemporary comparison of +23 gallons (Livestock Records Bureau, 1964)

Sample size	No. of samples	Sire estimates (gallons) Minus deviations 100+	50–99	1–49	Plus deviations 1–49	50–99	100–149	150+
10	105	6	6	23	33	18	10	4
20	52	—	—	31	38	31	—	—
30	35	—	3	23	48	26	—	—
50	21	—	—	10	80	10	—	—

Although the breeding operations of most pedigree herds are of no great interest in themselves, these herds are vital to the pedigree system as a whole, since it depends on having a large number of multipliers and commercial users of registered animals Commercial buyers contribute indirectly to breed society funds, partly by choice and, in Britain, partly as a result of official sanction against unregistered males. Multipliers are important as direct contributors of subscriptions, registration fees, and advertising costs and as buyers of stock from "superior" herds and flocks They are financially essential and any change which reduces the social cachet of pedigree breeding or which reduces their numbers is bad for breed societies and the pedigree system.

D. Breed numbers

Stonaker (in Hodgson, 1961) has described the changes in popularity of breeds of livestock in the United States as measured by the numbers of registrations in herd books. Since 1930 the total annual registrations in all beef breeds have risen from about 200,000 to 800,000, that is by a factor of four. During the same period the total population of beef

cattle has climbed from 27 to 65 million—roughly by a factor of two-and-a-quarter. Hence the proportion of all cattle that are registered has been rising. At present about one calf out of twenty-five born is registered. The Shorthorn which once accounted for 65% of all registrations now contributes a mere 5%; its place has been taken mainly by the Hereford. Latterly, the Hereford has had to make room for the expansion of Polled Herefords, Aberdeen-Angus, and half a dozen new breeds.

Dairy cattle in the United States reached their peak numbers about 1943 since when they have slowly declined. Registrations, however, have been mounting steadily, and exceed 400,000 from a total dairy cattle population of about 30 million. Most of the increase can be claimed by the Holsteins. In fact the other breeds have tended to attract fewer registrations since 1950.

TABLE 7.2

Numbers of bulls licensed in Britain since 1931 in 5-year periods (in thousands)
(compiled from Ministry of Agriculture sources)

Period ending	Ayrshire	Friesian	Shorthorn	Angus	Hereford	Total
1937†	16	9	88	11	8	133
1942	24	28	114	10	10	187
1947	37	48	81	7	8	180
1952	38	43	45	9	9	144
1957	26	38	26	13	11	144
1962	21	33	12	12	15	93

† Four years only.

Although registrations of females do not always parallel those of males, breed fortunes in Britain can be conveniently followed in terms of the numbers of young bulls officially licensed in England and Scotland These are shown in Table 7.2 for a few selected breeds of the greatest numerical importance. Until 1944 the Ayrshire and Friesian were expanding at the expense of the Shorthorn; thereafter all three began to contract as artificial insemination made itself felt. By 1962, less than half the number of bulls licensed in 1942 were required. Not all the reduction is attributable to artificial insemination since in recent years small herds have been disappearing at the rate of 3000 to 4000

a year and their demand for bulls with them. In spite of these changes, the two chief beef breeds have been relatively prosperous.

Pigs and sheep are no less susceptible to changing popularity. Some data illustrating the point have been culled from more extensive information given by Byerly (1964) and appear in Table 7.3. Although it would be interesting to know the causes of the rise and fall of breeds, they would be difficult to trace accurately. No doubt they include changes in market demand (for example, leaner hogs), show successes or

TABLE 7.3

Purebred registrations of swine and sheep in U.S.A. (Byerly, 1964)

Swine			Sheep		
Breed	No. of registrations		Breed	No. of registrations	
	1946	1961		1946	1961
Berkshire	24,628	14,138	Hampshire	31,875	29,586
Duroc	84,413	60,542	Rambouillet	13,433	9047
Spotted Poland China	43,731	13,020	Shropshire	22,100	9466
Landrace	—	27,307	Suffolk	6489	37,910
Yorkshire	3500	28,111	Columbia	3200	10,000
Hampshire	41,663	54,675	Corriedale	11,857	15,901

lack of them, advisory and extension work, and the effectiveness of breed propaganda. Whatever may be the exact combination of causes, the effect of both rising and falling numbers on the finances of breed associations is obvious. As income grows, more publicity of all sorts can be undertaken to ensure still more growth while a shrinking budget forces on members the inactivity that will make matters worse. It is worth noticing that once past the formative stages a breed which has failed to grow in numbers or to keep pace with its principal competitor rarely recovers or notably expands its popularity. Dominant breeds tend to give way to something new, not something old.

E. Breed Improvement

As Robertson (1963) has observed, breeds can be altered from within only slowly whereas buyers can change their minds quickly. A breed can be effectively dead before anyone realises that it is ill. When buyers change their allegiance, they do not leave behind the enthusiasm, the capital, or the time to make the deserted breed competitive again.

Once a breed declines in numbers to the point where it cannot match the amount of performance or progeny testing of its chief competitors, its power to compete is sapped.

Unless there were a wholly unlikely unanimity of view about the objects of breeding and about the amount to be spent on data collection, the prospects that outlays on improvement would be recovered in a small market for breeding stock seem poor. Many of the small societies can have no real interest in improvement. They are small because the breeds they support have little economic importance and until they acquire it, costly efforts to breed new models cannot be anticipated.

It would appear from past history that at any one time many breeders are investing in the wrong breed or the wrong ideal. Most breeds are either static in numbers or shrinking, and, while it is not impossible to make money in a falling market, a rising market usually provides the better investment. Although a long view is necessary for a constructive breeder, especially of slowly reproducing cattle, the short-term prospect of financial advantage from the sale of registered animals at a premium over the price of similar but unregistered animals must be the main attraction for most members of breed associations. When grade stock are equal in performance to registered animals, the ethics of this practice seem dubious. How many pedigreed animals would be required solely for breed improvement is a question that could only be answered by deciding the aims and the effort to be put into it. For artificial insemination organisations this question is by no means academic.

Left to themselves, large animal breeders would still disregard genetics for it is neither convenient nor economic for them to practise what it preaches. After 1945, however, the technological revolution made itself felt in livestock breeding. Of the numerous developments taking place, artificial insemination was the most conspicuous. In the post-war years there was a large increase in the number of men trained in genetics and physiology, who were inspired by the potentialities of artificial breeding and able to exploit the resources now in their hands. They had machinery which could cope with vast amounts of data, and they had the means to publicise their findings and opinions. Artificial breeding centres had to be efficiently and economically run, and they had to have some sort of breeding policy in which the features of the old craftsmanship could have only a minor part. In due course, the disagreeable truth came out that breeders did not know, in fact, how to select bulls able to increase yields. Their self-delusion was exposed by the progeny test. Pig breeders suffered the same fate, and sheep breeders can presumably look forward to it.

During this period, poultry breeding began its astonishing metamorphosis at the hands of a combination of geneticists and business men. In its present form, the poultry industry has little use for pedigree breeding in the sense in which this term is used for larger animals. This is not to say that the whole apparatus of pedigree breeding of cattle, sheep and pigs should be allowed to fall into decay. By and large, the turn of events seems to have caught breeders collectively unprepared for changes. Years after the warning signals were first flown, resentment still paralyses good judgment. Paradoxically, therefore, it falls mainly to those who have been the instruments of modernisation to consider carefully what role predigree breeders could play, that would give them a reasonable return for their efforts. There is no point in parading ancestral breeders, or in claiming virtue for past performances. At its crudest, the question is whether their current assets can be put to good use.

What are these assets? Numerically, pedigree breeders comprise perhaps 5% of all breeders. Financially, their societies tend to be weak and rarely able to conduct operational research bearing on their own efficiency and survival, or to hire trained scientific staff of a calibre to compel respect. Technically, they have their pedigrees and their associated systems of identification and some other records, and a market for breeding stock dependent on the diminishing goodwill of commercial breeders, extension workers and educators Socially, they comprise loosely organised groups of farmers with an interest in breeding. This last item is possibly the most important.

These general assessments of course do not apply equally to all countries and all breeds. Danish and German organisations, for instance, differ considerably from those in the United States and United Kingdom. Furthermore, breeders of sheep and beef cattle who have not yet felt fully the disenchantment with pedigree breeding, may be more inclined to overvalue their pedigrees, their stock, and their status, than are breeders of dairy cattle and pigs. (Robertson, 1963; Rae, 1964).

Since the days when it was written into the constitutions of breed associations and societies that improvement of their breeds was an objective, much has happened to make them act as relatively conservative bodies. Improvement, as they define it, to be sought at the rate they find convenient, however, is no longer acceptable to a generation with scientists, artificial insemination, computers, publicity and finance at its command. What was once an institution leading the way to better livestock, is becoming a brake on progress. Except in the numerically large breeds, societies achieve little more, from a public point of view, than a numbering system and the preservation of some

breeds, that might not be missed if they failed to survive. In the largest breed associations, the great mass of subscribers have no special significance unless the few breeders of elite herds and flocks are in fact improving their stocks. Of this, there is remarkably little evidence that does not emanate from them. Were all breed records, by some mischance, to be lost, it would not matter much, except to the herd owners concerned and perhaps not even to them. They would promptly re establish the numbering system, appoint themselves the arbiters of new elite herds based on unregistered purebreds, and in a short space of time all would be as before.

It is probably necessary to add that these remarks arise from the fact that in countries with highly developed livestock industries, there is now little difference between registered and unregistered animals of the same breed. Furthermore, the problem of deciding what constitutes improvement should not be one for constructive breeders alone. Their ability to make slow changes in type is not in question, but their ability to define objectives, control modern resources, and cope with invisible traits, is highly suspect, unless they have power over very large numbers of recorded animals. If they can acquire this power, and remain constructive breeders, they will have no need of a breed society. From the point of view of the livestock industry as a whole, the real danger is that those who do exercise control over large numbers may saddle themselves with the inhibitions of pedigree breeders without their reasons.

process has not gone so far in pig breeding, and is not very evident as yet in sheep breeding, excepting the Merino in Australia and the Romney in New Zealand. Although economic forces may cause other breeds, at present relatively less popular, to displace the present leaders, it becomes progressively more difficult for them to do so, unless they can command sufficient modern publicity. The advantages of size and big numbers are not easily overcome. Large populations of animals support effective advertising and exhibiting and they are more likely to include some herds run by owners exceptionally gifted in some relevant way. Where a change of direction in breeding needs to be brought about quickly, they offer more opportunity of finding suitable animals. The idea that there is a critical mass which has to be exceeded before a breed generates enough activity and energy to become competitive is attractive, but measures for improvement probably depend not only on numbers but also on their rate of increase and the intangible element of enthusiasm.

Assuming a widening interest among commercial farmers in performance-tested stock, the large breed associations would be in a strong position to provide, if they wished, this kind of stock, whereas it would be practically impossible for the small ones to do so, unless the financial burden were to be carried by some other body. The same principle applies to milk recording in most countries, and it might well apply to spending money on the testing of numerically small breeds, especially the offshoots of large breeds. Indeed, testing could be the key to success for a new breed. By the same token, testing could damn a breed as inferior. Testing as a technique for improvement, however, has a value which increases with the numbers available for testing and selection, so that there ought to be some non-linear relationship between outlays on testing and the degree of improvement. Where these outlays originate in public funds, there is the additional question of the proportions which should be spent on sheep or pigs or other classes of stock. If there are official policies in the Western democracies implying answers to these questions, they do not seem to have been publicised.

When money speaks clearly enough, it is remarkable how quickly breeds can sometimes respond, notwithstanding all the handicaps of small scale operations. This follows when breeders become united in striving for a simple objective. Changes in length of bacon pigs, and reduction in fatty deposits of sheep, pigs and cattle take place rapidly when quality differentials are paid. These traits have a moderately high heritability.

Where many small selection lines are being carried (that is, individual

herds) some will proceed much faster than the statistical average for a large population. If breeders are agreed on objectives, and the objectives are simple enough, recognition of superior stocks can lead to rapid advances. The usual difficulty is that the condition for such progress, a high selection differential, is not met. Superior stock does not turn up in the top herds, or is not recognised, or the objectives are too complex for rapid change even in small lines. Given a relaxation of type requirements, however, good progress could be made in spite of low heritabilities, provided the wish were there. It is not genetic theory which is at the root of controversy, but the rate at which breeds will be allowed to become obsolete. Like politics, improvement of livestock is an art of the possible.

Convenient though it may sometimes be for protagonists and antagonists of breed associations to discuss them in extravagant terms, general statements about their present or future value seem scarcely advisable. In the past there has been so much evolutionary diversity, that, both between and within countries, the functions exercised by breed associations vary widely. If they ceased to exist, some other body would have to be invented to register births and parentage; but it would not necessarily select the same animals to register, or conduct propaganda. Given the stimulus of a livelier interest in economic traits and the threat of competition from splinter groups, some breed associations will no doubt evolve further.

F. Possible *reforms*

Since breed associations regard themselves as essential components of a national industry, it is perhaps not out of place to recall some of the suggestions that have been made for their reform. Prosperous associations tend not to take kindly to such suggestions, but the weak and apprehensive bodies are more receptive. Obviously, those who try to be helpful are interested in the vitality of breed associations as constructive forces in animal breeding and not as private bodies pursuing

complaints. Protecting business interests is less important than breed improvement, yet some breeders tend to oppose rather than collaborate in the use of artificial insemination and performance testing which could help them. Discouragement of this sort eventually drives progressive breeders out of breed associations.

TABLE 7.4

Approximate operating expenses of breed associations per registration in 1963

Breed	U.S.A. No. registered	$	U.K. No. registered	£
Aberdeen-Angus	345,600	33 9	6300	5·4
Hereford	513,000	3·1	20,300	1·9
Holstein Friesian	259,000	6·4	82,000	1·7
Ayrshire	14,600	11·8	41,000	1·0
Jersey	42,400	13 3	23,100	1·7

Pedigree breeders need modern techniques if they are to stay in competition with the large corporations. They can have ready access to the modern tools they need if they are willing to pay for them. As an example of what can be achieved, the Swedish Livestock Management organisation repays study (see Fig. 5.1). The average amounts spent by breed associations for each animal registered vary widely. Publicity, field officers, prizes, research, performance records, and administrative costs show an uneven incidence and consequently the ratio of total costs to total registrations, as given in Table 7.4 for a few breeds varies correspondingly. This table may serve, however, to give some idea of its order of magnitude. The figures may be compared with the difference in value of registered and unregistered stock, provided the breeder's own costs of advertising and other expenses are not forgotten. None of the values shown are strikingly large relative to the value of the animals. They would have to be increased to finance performance testing.

2. getting rid of the burden of keeping and publishing long pedigrees;
3. organising breeders groups to enlarge the effective size of breeding herds and flocks;
4. putting greater emphasis on economic merit;
5. exploiting the facilities available for data collection and analysis, advice, publicity, performance testing and artificial insemination;
6. discarding the narrow approach to pure breeding;
7. constructively using crossbreeding and importation.

In addition to submerging the individual in the group, most of these actions involve parting with some independence.

If an object of a society is to help to ensure the growth of capital and interest on the investment of members in pedigree stock, members had best take an objective rather than an emotional view of artificial insemination, fairs and shows, performance testing, propaganda, purity of pedigree, type classification, herdbooks, livestock exports, breed councils, and genetics. The problem before them is, perhaps, not whether amateurs or professionals should control the apparatus of livestock breeding, but how both may use it to advantage.

V. Geneticists and Breeders

In the course of the discussion, contrasts and conflicts between scientists and practical breeders have been repeatedly pointed out. To conclude the chapter dealing with breed associations, it may be appropriate to return once more to this theme.

There are three strata of active participants in animal breeding at the decision-making level. There is first of all the professional research geneticist employed by the state or by a university. He has a vested interest, not in industry, but in the genetic concepts which he or his teachers have formulated. He may have difficulty in freeing himself from them and in becoming objective, should a total evaluation of breeding theory be required.

He has his counterpart in some industrial establishments, particularly those dealing with poultry breeding. Although the commercial professional geneticist may be more flexible in his thinking and be more readily swayed by economic facts, it is probable that industrial geneticists are more dogmatic than the academics. This arises from differences in personalities between the two groups which choose these divergent careers and even more so from the divorcing of the practising industrial geneticist from the academic atmosphere of untrammelled enquiry.

The managerial stratum is next. Here are men of both worlds such

as are probably found in any other type of industry, as well as in agriculture. Although sometimes in positions of administering quasi-government agencies (and here again a Milk Marketing Board comes to mind), they may have come through a training in biology and have often more open minds than many businessmen.

Finally, there is the practical breeder. Once more, the poultry industry is the exception to the general rule. In it, geneticist-managers have taken over the direction of breeding policy in most if not all advanced countries. It is only a matter of time before the same will happen in under-developed areas. But, in the larger classes of livestock, the biologically untrained men are still in charge and the differences in background, in outlook, and in sophistication between them and the academic or research biologists, needless to say, leads to mutual antagonisms

It is possible that geneticists underestimate many practical difficulties in their simplified theoretical concepts, but it is certain that many breeders refuse to understand and to credit the geneticists with having advanced their cause in any way. And the genetic views of small breeders, agricultural journalists, and, in many relatively backward countries, agricultural college staffs trained in the non-experimental or field-trial tradition, abound.

The usual question asked by the breeder of the scientist is what genetics has contributed to animal breeding. The accomplishments of a Bakewell, and other eighteenth and nineteenth century practitioners of the art are cited in contrast with those of the modern population geneticists, and the work of the practical plant breeders, alleged to have produced remarkable varieties of alfalfa, wheat or fruit, is often favourably contrasted with the contribution of geneticists to animal breeding.

It is essential to counter these accusations, not in order to justify the work of research geneticists or to put control of breeding policy into their hands. The importance of a rebuttal lies in placing their work in proper perspective, since future decisions, which will affect most of mankind, will depend on it. It is essential to point out what the scientific approach is, why there is a necessity for quantitative and precise measurement instead of the guessing characteristic of the pre-scientific days of breeding, and why there is a need for a rational, instead of an emotional, evaluation of the requirements and the directions of future livestock breeding.

Large scale operations of breeding, which *nolens volens* most of the world is forced to adopt for the sake of efficiency, depend now on the quantitative approach to the only three variables that anyone, practical

breeder or academic geneticist, has been able to devise as the basis of genetic improvement of diploid sexually reproducing animals: (a) the choice of parents, (b) the selection of the way in which the males and the female parents are combined in mating, and (c) the number of offspring that a chosen parent is permitted to contribute to the next generation. All of these have to be rationally and quantitatively manipulated for the sake of speed and efficiency. The present population genetics theory may be a relatively poor thing and is certainly susceptible to improvement but it is vastly superior to the rules-of-thumb of the early breeders who could not do the job they did 150 or 200 years ago on the scale which is demanded by the exigencies of today.

The early breeder most certainly chose parents largely on the basis of phenotypic excellence as determined simply by his eye. When progeny testing was introduced (and this may have been of biblical antiquity), the choice of the animals to be tested still had to be based on the phenotype, and the use of pedigrees, which came in later, cannot be shown to have contributed a great amount to the efficiency of breeding practice. But the principle of using parents, themselves undistinguished in appearance but able to combine well in crosses, derives from post-Mendelian experiments This systematic utilisation of hybrid vigour in animal improvement, although put into commercial practice by breeders was based on genetic research Genetic theory is playing a vastly more significant part in animal breeding than many practical agriculturalists realise in spite of the changes it has wrought in the aims, the methods and the structure of their own industry No conglomeration of individually small operators can produce the genetic improvement of which a large concern is capable, unless they band together and so become large themselves. In short, the task of breeders as well as of professional research geneticists is to adjust their operations to the needs of the present and the future so that they can contribute not only to their own personal welfare but to that of humanity.

Part IV: The Future of Animal Breeding

CHAPTER 8

OPERATIONAL PROBLEMS

Organisational changes as extensive and fundamental as those now taking place have numerous consequences. So it comes about that stockmen must learn to talk with mechanics, and auctioneers, to read statistics. Journalists have their own adjustments to make as do the nostalgic elder statesmen of agriculture. However, only a few of the problems that arise can be discussed here and then only briefly. They fall conformably into two classes: those presenting themselves as a result of the expanding demand for the prompt solution of practical problems by research, and those that come of thinking in terms of individual animals or of herds and flocks.

I. The Explosion of Scientific Information

Since the last war there has been a rapid increase in the amount of scientific effort expended by both public and private agencies. This has brought its own difficulties, for the faster progress has meant a high rate of obsolescence of research equipment. More serious still is the obsolescence of research workers and teachers which now amounts to a galloping disease. Although there is much inconclusive worrying about this problem, no radical solution to it is in sight. In the paragraphs which follow some of its salient features have been described with the aid of Price (1961, 1963), Dedijer (1962) and reports of the National Science Foundation (1961, 1963). Many other sources have also been consulted.

It is generally agreed that the human population now doubles itself approximately every thirty-five to forty years. Yet the doubling time for the number of scientific journals and for scientific papers published

is estimated to be at the most fifteen years (shorter in countries only recently developing their scientific effort). The doubling time for the number of scientists and engineers (U.S. estimate) is close to ten years; that for total expenditures for research and development is about six years; that for expenditure per head varies from about two years for China and Japan to five years for the United Kingdom, the United States, and Canada. In Commonwealth Agricultural Bureaux Journals, the number of abstracts has gone up from 25,661 in 1946 to 61,474 in 1962. Since some of the increase is due to better coverage, it is safe to conclude that the rate of expansion in numbers of scientific papers in applied biology is rather less than in physics and chemistry, but it is still formidable. In animal breeding, the growth rate is less spectacular than in many other fields, but nevertheless rapid. Thus, for Animal Breeding Abstracts, the annual number of papers abstracted has risen from 1200 to 3600 over the last twenty years, but the amount of material in the *Journal of Animal Science* has increased some six-fold from the first volume published in 1942 to the last complete volume in 1964.

Among the fascinating implications of these and similar figures which have been brilliantly explored by Price is the fact that about 87½% (an estimate of 93% has been made by others) of all scientists who have ever lived are alive and working today. The number of scientists listed in "American Men of Science" has increased in the last five decades from 5500 (60 per million population) to 96,000 (480 per million). Because of the increase in the frequency of multiple authorships of articles, the total number of papers may not have multiplied at a similar rate, but its rate of growth is still staggering, especially since every author will apparently produce on the average 3·5 articles (the individual record of 995 items in one person's bibliography seems to be held by the British mathematician Arthur Cayley).

In addition, a great diversification of sources of scientific information is occurring The unchecked flood of new textbooks, symposia, proceedings, reviews and monographs is threatening to defeat its own ends. Thus the number of scientific journals has risen in the last two centuries from 10 to about 100,000, and no slowing down of the rate of increase is evident although a ceiling somewhere must be supposed to exist.

other aspects of research. Irrespective of their choice, they are bound to fall steadily behind their younger colleagues relative to the state of knowledge and in comprehension of new ideas. Given the fact that in the realm of animal breeding research experiments may take a dozen or more years to complete, this state of affairs obviously threatens the pursuit of livestock investigations. For one thing, it may be found that by the time all the data of an experiment are in, the methods and designs used, and possibly its very objectives, are out of date. For another, recruitment of professional personnel of high competence is jeopardized, if the satisfactions that scientists obtain from successful solutions of problems are withheld in this manner from them.

A similar state of affairs might be expected to occur also among scientists working in industrial research and development, Surprisingly, this is not necessarily the case in all fields. Kovach (1960) has presented graphs showing that whereas the lag between the date of a discovery in mathematical theory and its application is increasing (fifty years in 1860 as against seventy years projected for 1960), that between scientific discovery and engineering application is dramatically being reduced (sixty years a century ago but only three or four now). Indeed, in animal breeding practice, the lag may even be negative with application, on occasion, preceding scientific formulation or explanation. The use of inbreeding in breed formation for instance, took place long before the mechanics of attaining homozygosity were understood; and so did the utilisation of heterosis, the genetic basis of which has still not been completely elucidated. This means that in contrast with their colleagues in universities and research institutes, geneticists working in industry can commonly not only reap greater financial remuneration, but are also likely to obtain more of the less tangible satisfaction of seeing the fruits of their labours early. These are factors with an adverse bearing on the incentives for productive and creative scientists to engage in basic research on animal breeding.

The fact that the bigness of science is affecting scientific methodology and the direction which research takes is indisputable. In animal breeding research specifically, accurate world-wide data showing how big the field has become are not available, but it is possible to give some figures of overall expenditures by governments and by industry for research and development.

These data have limitations, some of which arise from the definitions used to distinguish between basic research, applied research, and development. For present purposes there seems to be no need to split hairs. The broad definitions used in the various reports of the National Science Foundation can be accepted. In them, research is described as

systematic, intensive study directed towards further knowledge of the subject studied Basic research addresses itself towards increasing knowledge Mendel's experiments would fall into this category. Applied research is directed towards practical applications of knowledge. In this sense, investigations on the use of Mendelian principles for practical ends, for example, transforming horned into polled breeds of cattle, would be termed applied research. Finally, development refers to the systematic use of knowledge for designing and producing useful prototypes, materials, devices or processes. The creation and improvement of a polled breed prior to its release to farmers would be designated as development.

TABLE 8 1

Expenditures on science in different countries (from Dedijer, 1962)

Country	Year	Research and development expenditures	
		as % of gross national product	per caput in U S $
U S A.	1960–61	2 8	72 4
U S S R	1960	2 3 (?)	36 4
U K.	1958–59	2 5	26 0
Sweden	1959	1 8	24 3
Canada	1960	1 2	21 9
France	1961	1 3	15 2
Australia	1960–61	0 6	8 9
Japan	1960–61	1 6	6 2
Yugoslavia	1960	0 7	1 4
China	1960	?	0 6
Ghana	1960	0 2	0 4
Egypt	1960	?	0 3
India	1959–60	0 1	0 1
Pakistan	1960	0 1	0 1

Table 8.3, where it may be seen that the investment by the U.S. government in research and development activities went up from under \$10,000 million in 1961–62 to well over \$16,000 million in 1965.

TABLE 8.2

Total expenditure for research and development, 1961–62, millions of dollars (from National Academy of Sciences, 1965)

Sources of funds	Research and development performers: Federal government	Industry	Colleges and universities	Other non-profit institutions	Total
Federal government	2090	6310	1050	200	9650
Industry		4560	55	90	4705
Colleges and universities			230		230
Other non-profit institutions			65	90	155
Total	2090	10,870	1400	380	14,740

The growth of research in agriculture is shown in Table 8.5. These sketchy data provide at least the general financial background against which animal breeding research may be viewed. Admittedly, space, military, atomic energy and medical research attract vastly more support than does that in agriculture. But the point to be made is that

TABLE 8 4

Distribution of scientific expenditures in Britain (from *Anon* , 1962)

	In %			
	Basic research	Applied research	Development	Total
Government departments (military)	1	19	80	100
Government departments (civilian)	5	45	50	100
Atomic Energy Authority (civilian work only)	20	50	30	100
Research councils	40	55	5	100

TABLE 8 5

Expenditures on research by some government agencies (from National Academy of Sciences, 1965)

	Year			
	1947–48	1956–57	1960–61	1962–63 est
U S Department of Agriculture, millions of $	39	88	131	160
U K. Agricultural Research Council, millions of £	0 9		5 6	6 5
Scottish Department of Agriculture, millions of £			3 7	4 6†
French National Agricultural Research Institute, millions of NF		9 0	29 0	37 6

† Includes advisory service

research expenditures on the scale of 1 to 3% of the total national income are possible for all but the most undeveloped countries. Whether this amount is spent for developing armament, for reaching the moon, for research on limiting population size, for a search for cancer cures, or for work on increasing food supplies, is a matter of choice for individual nations or for supra-state organisations. The policies governing expenditures of this magnitude must, of course, be considered from many angles with which the present discussion is not concerned. For a fuller account, readers are referred to a report of the National Academy of Sciences (1964).

II. The Tactics of Animal Breeding Research

The investigations of the Lush school, although taking into account non-additive genetic variability, addressed themselves primarily to the additive variation which is amenable in some degree to straightforward selection. More attention has recently been paid to the theoretical bases of other types of variation, notably those involved in heterosis. It seems, however, that the law of diminishing returns is beginning to assert itself in this approach to problems of livestock amelioration. Refinements in the statistical theory of genetics, as well as in the estimates of parameters of concern to breeders are still being made. But they seem to be mainly of a technical rather than of a conceptual kind, and it may well be asked whether or not the time has come to consider completely fresh avenues of attack on the unknown in animal breeding. The question has acquired some piquancy because suspicions that early claims implying that population genetics could solve all problems of animal breeding were exaggerated, are being entertained now even by their warmest advocates.

Only a few years ago Lush (1960) himself surveyed problems of dairy cattle improvement which require further information for solution. It is somewhat distressing to find that, with a few exceptions, they refer to the very same issues that could have been listed, say, fifteen years earlier. They are:

1. Information on values to be used in selection indexes, that is, heritabilities and economic weights for each of the traits to be considered, and genetic and phenotypic correlations between them.
2. Separation of epistasis from overdominance effects.
3. Examination of the possibilities of rotational crossbreeding.
4. Possibilities of improvement by selection for combining ability.

5. The significance and possibility of utilising genotype-environment interactions.
6. Problems of data collection and processing.
7. More accurate statistics on natality, mortality, sterility and other relevant properties of populations.
8. Techniques of creating new breeds.

Lush also refers to artificial mutagenesis, but in such pessimistic tones so far as cattle are concerned as virtually to exclude it from the list of prospective research projects.

There is little doubt that all of the topics in the list are worthy of continued attention. How many of them should fall within the province of state-supported research is, however, an issue. The list is presented here merely to highlight the point that, useful as the population genetics approach has been, and fruitful as it may continue to be, in itself it does not now offer many opportunities for threshold developments, a succession of which is necessary for research to thrive. It has been validly said that the greater part of scientific drudgery consists of mopping-up operations. All of the eight points listed are manifestly of this type and are unlikely by themselves to lead to important fundamental discoveries.

Such discoveries are not arrived at merely by wishing. The time must be ripe for them to occur. There must be the right people to recognize where they may appear, perhaps to seize on an anomaly, perhaps to attempt a new synthesis of observations or disciplines, perhaps to catalyse the work of others The recent great advances in genetics seem to have come about in great measure by the intervention in biology of physicists, crystallographers and chemists, bringing with them fresh and uncommitted outlooks Indeed, an historical example of such cross-fertilisation is provided by Sewall Wright's own short excursion from strictly zoological and evolutionary pursuits into animal breeding. The question then arises how a new phase in animal breeding research can be encouraged to begin and where it may be expected to take place

The answer to the first of these questions, at least in part, depends upon that to the second since there are now several types of research agencies and for each of them a different reply may be appropriate. These include

2. Research units supported in part by state funds and eligible to receive subventions from private money-granting foundations or agencies. These are usually connected with University or Agricultural College departments, and are the most widespread type of unit for animal breeding research in Europe and America.

3. Private institutions engaged in research as a public service. The Rockefeller Foundation with its work on Latin-American agriculture is an outstanding example of this kind.

4. Statutory institutions, the primary function of which is production or marketing but not research, though part of their income may be devoted to research either directly or by supporting other agencies. The Milk Marketing Board of England and Wales is one example of such an organisation.

5. Private industry. Compared with non-agricultural and some agricultural industrial businesses (e.g. in stock nutrition, veterinary medicine or ornamental horticulture) those dealing with animal breeding still devote a pitiable amount of their expenditure to research and development. The outstanding exception is the poultry industry, which, both in the United States and increasingly so in Great Britain, is investing very heavily in this activity. It may be expected that similar developments will occur in other classes of stock in due course of time, especially if commercially sponsored research institutes are extended to this field as much as they already are in the physical sciences.

The two latter types of agencies are at present devoting their efforts primarily to development and not to basic research. At best, they can be expected to carry out research on specific methods and techniques of improvement of their product or on the principles governing the biological properties of their own stocks. There is a paradox here in that research findings are, generally speaking, of much less value to small scale producers than to large ones, and, consequently, science may even work to their personal disadvantage. Indeed, the original intention behind the public financing and administration of agricultural research was to help an industry composed of relatively small productive units. But by now, the picture has changed so that at the moment it behoves the first two kinds of organisations to devote themselves to basic research, to investigate general principles, and to tackle speculative, imaginative "far-out" problems, ideas and experiments. State-supported institutions should be encouraged to search for breakthroughs. And if they are to do so unhindered, responsibility for some of the applied research might be delegated to the other kinds of agencies as they become intellectually and financially able to support it.

It has been said by Pavitt (1963) that "in the industrially advanced countries the long-term, risky and often costly investment in research and development, and the often imperfect knowledge of industrialists as to its potential profitability, make it highly unlikely that an adequate level of expenditure on research and development for economic purposes will be achieved without governmental encouragement and aid." As far as livestock improvement is concerned, this point seems well taken.

It should be understood that, since as yet much of the agricultural production in the capitalist world is carried out by individuals, co-operatives and companies which operate on too small a scale to afford extensive applied research and development, governments (as suggested by Pavitt) might aid and advise establishments largely financed by individual companies but carrying on research and development that would benefit the industry as a whole.

Clear-cut distinctions between basic and applied and developmental research projects are notoriously difficult to make and to commit large research laboratories exclusively to one kind would usually quickly prove foolish for various reasons. For one thing, recruits, even if so cleverly chosen that all are skilled at basic work to begin with, will not all remain so. For another, a project may slip rapidly in either direction so that the original classification of either the project or the workers on it cannot be maintained Some projects are primarily for educating the people who carry them out Others are to maintain an active corps of able technologists who can apply and adapt advances made elsewhere Still others may serve as an insurance against the risk that some advantage in technique or resources will accrue exclusively to a competitor. Notwithstanding all this, it is possible to place varying degrees of emphasis on the several stages of research. What is now suggested is that, as livestock breeding becomes more organised, development and operational work will fall increasingly to the industry itself to support, whilst basic and applied work will continue to depend on taxpayers.

No recipe guaranteed to result in a breakthrough is known, but a number of ingredients can be given The first would be the abolition of specific crop-oriented research units in institutions where they exist. If departmentalisation is necessary in agricultural colleges, functional designations, such as genetics, physiology, nutrition, would be more profitable that commodity ones, such as dairy husbandry or poultry science The principles of breeding apply to all species. Whatever the organisation of the intra-institutional units, no impediments to cross-departmental flow of staff activities of ideas and of co operation between the units should be permitted.

There should be freedom but not licence to explore any byways that a responsible investigator may wish to follow. There have to be limits, and budgetary costs of experiments have to be kept in line with the total resources of an institution. But only broad administrative restrictions on the approaches used, the materials employed, and, indeed, upon the aims of the experiments need be exercised. In choosing the scientists who would have such scope and independence in their activities, much care has to be exercised. Imagination must be tempered by intelligence, and non-conformity by purposefulness. As a desirable counterpart to such men, there should be others of sober judgment, and scientific conformity. No applied, operational, or developmental research can flourish without a solid underpinning by fundamental work. Developments in the United States have prompted Storer (1963) to say: ". . . we must expect to find that basic research will become the tail rather than the dog in coming years. Unless knowledgeable efforts are made now to protect it we may find it being wagged right off the dog without our being aware of it . . . when applied research comes to dominate science, it will come under the guise of basic research."

Experts in non-biological subjects, or in biological disciplines other than genetics, could be encouraged to join the staffs of these research institutions. If the motivation for scientific work is either pleasure or gain, opportunity for one or the other, if not both, must be supplied for recruits. All of these conditions simply mean great flexibility in administrative matters.

III. Contract Research and Consultants

It is now possible for anybody to engage the services of experts or consultants who will advise on many aspects of business administration and organisation. They will conduct surveys of consumers, advise about advertising campaigns, and how to make the most persuasive charitable appeals. There are institutions which are well equipped and willing to carry out contract research. This is a form of activity which is somewhat more highly developed in the United States than it is in the United Kingdom, and it seems likely that it will grow for the simple reason that not all business firms would find it worth their while to establish research laboratories to carry out what might be an extremely specialised or short-term investigation. At the moment there seem to be few institutions of this kind for servicing the agricultural industry. In most countries farmers have come to depend on state-aided institutions for investigating their problems and giving them advice. It is doubtful whether either applied research or development in the field of livestock

improvement can any longer be handled entirely in this way. This is especially so in the operation of breed societies or associations where the position is rather unsatisfactory. If they depend on advice from research institutions and colleges, one or other of three things is likely to happen They may get good advice which they can understand and apply; they may get good advice which is couched in indigestible and unacceptable form and is like corn sown on stony ground; or they may get bad advice which arises from the fact that their problem has been insufficiently studied by someone who has other things to do, and is not being paid for his efforts or lacks sufficient personal incentive to finding the best solution. It may be that in the future, as university institutions occupy themselves with fundamental work, industry would be well advised to make greater use of contract research.

The concept of contract or sponsored research dates back to 1886 although the first sponsored research institute was not set up until 1911, following the establishment of industrial fellowships at the University of Kansas. There are now numerous commercial laboratories and a few large institutes such as the Battelle Memorial and the Arthur D. Little, Incorporated, which undertake sponsored research (Woodward, 1960). In some industries, chiefly those with a large content of modern physics and chemistry, contract research has expanded until it now employs thousands of scientists.

been anxious to expand their activities to crops or livestock which would require large capital outlays in farms and buildings. Their research has no direct advisory or teaching value. Some laboratories, however, do provide an advisory service through which experts, especially in operational research, can be obtained.

For people and firms in the agricultural industry who are not accustomed to the real costs of research, the expense of contract research is likely at first sight to appear alarming since research projects have to carry their proper share of the overhead costs. Nevertheless, contract research is now highly developed in the United States and in spite of some disillusionment due to too optimistic views of its possibilities and its use in unsuitable circumstances, it is likely to grow much more. Meanwhile, it is expanding rapidly in the United Kingdom, in Norway and Germany and other European countries where research associations have often failed to thrive.

A prerequisite for the successful use of contract research is that there must be somebody with a problem. It is not necessary that the person or institution should be aware that there is a problem, but should be capable of becoming aware. That person or company must also be interested in having the problem solved and in acting on the results. The solution, however, may turn out to have consequences which management had not foreseen and does not wish to accept. It goes without saying that whoever wishes to benefit from contract research, must be willing to pay for it.

Business enterprises, government departments and large scale organisations of farmers are already using contract research for many purposes. Agriculture is moving gradually away from the small individual enterprises towards organisations big enough to finance contract research on problems that directly affect their running. Its growth starts slowly however, not only because the demand for it has to develop, but also because its success depends on acquiring temperamentally suitable scientists of great skill. Normally, such people can find very attractive occupations either in industrial laboratories attached to large corporations or in universities. Hence, the success of contract laboratories is likely to be measured by the rate at which they can acquire the men needed.

There seems no doubt that in the newer types of agriculture there will be plenty of room for solving *ad hoc* problems in biology and in applying operational research techniques Producing, distributing and packaging of farm products seem to be no less and are probably far more complicated than those arising within other industries. Office administration, data handling and co-operatives also provide a very

fruitful field for the unbiased investigator. Furthermore, the shortage of good scientists in agricultural research institutions who are experienced in these matters on conjunction with the difficulties of switching them from one activity to another when they have teaching and administrative duties to perform, will place an increasing strain on the machinery for agricultural research.

Operational research was developed during the war as a result of an attempt to apply numerical thinking to wartime problems. Twenty years later it is possible to say that it has developed extensively in industry but is still in the process of discovering the appropriate scientific methods for combining the social sciences with the others whenever required to so in the solution of practical problems. The exponential acceleration of research means that each generation's life and uncertainties differ more and more from those of its forbears. Precedent is a less and less useful guide and consequently operational research faces an expanding volume of work.

Another method which is rapidly developing in the United States to meet difficulties is the use of consultants. Where these are completely independent they operate like contract research laboratories but where the consultants are members of the universities' staffs it is necessary to have some institutional agreement to their acting as consultants and to receiving the necessary rewards of their work. This is common practice in the United States (though not in agriculture) but in the United Kingdom, while the employees of universities are usually able to accept substantial fees, this is not encouraged in the state-aided research institutions.

genetics and animal breeding, at least one enterprise specialising in this field is represented in the Society. It is a consulting firm which will process data, set up breeding programmes and carry out specific analytic assignments for private individuals, associations of breeders and government research institutes which are attempting to solve some short-term problem. The species of animals in which the clients of this organisation are interested include chickens, turkeys, cattle, dogs, rabbits and several kinds of fish.

Should this type of sponsored research prove to be as satisfactory in the field of animal improvement as it has in chemistry and physics, it may be possible to organise small scale breeders who are willing to submerge their independence in a consortium large enough to compete successfully with the emerging giant poultry and livestock breeding companies. Little attention so far has been paid to biological problems and less still to social and motivational ones but contract research and consultation is a developing industry and it is likely to move into these fields more and more as time goes on. The discovery that business can conduct industrial research at a profit is an economic advance of the first order and it is by no means certain that the profit from better physical and chemical processes will be any higher than that from applying it to the biological and social sciences.

International Biological Programme have been in operation or are being planned. Finally, a great number of international scientific congresses and symposia, largely for exchange of information, are being held, often under the auspices of international scientific unions or councils.

TABLE 8.6

Types of international co operative enterprises (adapted from King in Goldsmith and MacKay, 1964)

Organisation	Number of member countries	System
CERN	13	Large centralised institution based on high cost of equipment
EURATOM	5	Separate laboratories in different member countries
ESRO	11	Co-operation between different laboratories (individual initiative)
ELDO	7	Division of labour between countries (politically organised)
ENEA	—	Independently managed and financed projects with central supervision
OECD	21	Common programming and voluntary collaboration but locally financed

may adversely affect the training of the younger scientists by removing founts of inspiration. This aspect of the matter could be partly remedied by the introduction of a rotational scheme of assigning all of the researchers in an international laboratory to teaching duties for periods of time in various member countries, independently, of course, of national origin. These teaching duties should not necessarily be in the form of lectures or university courses but could be adapted to the special talents of a given individual so that seminars, conferences, the writing of books, and the preparation of other instructional devices could be assigned depending on his special abilities.

Breeding research appears to be *adaptable to an international* scheme of operation. The costs of fundamental work with large animals, if it is to be carried out on an adequate scale, are prohibitive for many of the smaller countries which have recently acquired their independence. And yet these are the countries that need much research of this type on which to base their own applied work and development. Mere reliance on work done in the United States or the United Kingdom has adverse psychological effects both on the political morale and, in the long run more importantly, on the morale of the people who are responsible for development. Establishment of international research centres could provide for them a sense of participation. It would support a systematic exchange of visiting teaching personnel and would go a long way towards inculcating the scientific attitude and a sense of responsibility. But it might be exceedingly important not to permit such institutions to become toys for bureaucrats, a dangerous enough failing on the national scale, and possibly fatal when international co-operation is concerned.

There is no dearth of subjects on which research projects, either centrally established or carried out in several locations, could be undertaken economically and profitably. Principles derived from basic research must underlie development, and therefore the special directions that basic research takes should, if only in part, be a feed-back response to the needs of development. By pooling resources the have-not countries would have a better opportunity of obtaining the information on which development of their livestock breeding must depend.

Beyond this, there are many applied research problems that could be more readily solved on such a co-operative basis. For example, if genotype-environment interactions are, as many believe, an important limiting factor in the improvement of our livestock, the possibility of testing genotypes over a wide variety of environments is greatly enhanced when experimental stations working on the same problem are scattered, for instance, throughout the continent of Africa, instead

of located in only one country. There is also the possibility of using partial isolates or sub-populations with occasional interchange of germ plasm. This was considered by Wright to be the most efficient way of producing long range evolutionary change, and it could be exploited by pooling the resources of several countries. The introduction of exotic varieties and creation of unrelated inbred lines for crossing might be facilitated in the same way.

Finally, not the least of the benefits that may be expected would come from improvement of documentation, standardisation of data-publishing methods, increased reliance on a common language, especially for abstracts and, perhaps, the stemming of the uncontrolled tide of scientific journals by internationalising them.

V. Decay of Genetic Variability

It may soon become one of the implied responsibilities of any organisations or institutions which control the genetic destiny of a whole species to maintain a reserve of variation for further improvements and for unforeseen shifts in the environment or in demand. Indeed, it may be said that each generation has an obligation to see that genetic variation, like soil fertility, is not handed on to its successors in an exhausted state. The argument, however, that such reserves may be needed in case new diseases spread is only partially valid. In the past the advances made in veterinary science appear to have come more quickly than truly disease resistant individuals could be bred. The length of a generation in the larger animals means that pathogens could probably outpace selection for resistance (an argument first advanced by Haldane against the possibility of successful natural selection for infectious disease resistance). But it is, of course, possible that changes in environment, or extensions of the existing range of environments (and hence in the most efficient genotype), may be necessary. Such could arise, for instance, from mechanisation or intensification. Similarly, shifts in demand can be rather rapid and require rapid responses. An example of this type is provided by depth of backfat on pigs. Had there been no genetic variability in this character, pig breeders would not have been able to reduce the amount of fat by breeding when the market dictated this.

In closed populations some decay of genetic variability is inevitable. Indeed, selection advances must normally always be made at the expense of variability. Restoring genetic variance by artificial mutagenesis is a theoretical possibility, but as yet no demonstration that it is practical in domestic animals has been given. Furthermore, until

directed mutations can be induced, the undesirable changes simultaneously produced might make this too expensive to put into practice.

Breed or strain crossing, that is, introgression of genes from one population to another, presents more immediate means for renewal of variation. But its use involves the maintenance of separate strains, breeds, or gene pools. Whether or not a monopoly which has found one particular population to be the most successful money-maker would necessarily keep in storage other populations simply with an eye to the future, depends on the position of the horizon in its planning. It is readily conceivable that exigencies of a purely economic kind may require such organisations to discard their stocks even though originally their managers had fully intended to keep them indefinitely. This argument should not be construed as advocating the maintenance of all available and newly arising genetic variants. In the future genetic variation may be contrived as needed, if not by mutagenesis then by the use of exotic breeds, and hence it would be wasteful to regard every variety of livestock as a potential treasure house of genes to be preserved at all costs. Given Holstein and Jersey cattle, it is likely that every other known dairy breed could be reconstructed as closely as need be, and many more. For some time yet, much genetic variation will be preserved because of the innate slowness of evolutionary processes and, in the absence of regimentation, because of the wishes of breeders who pursue breeding policies of their own independently both of breed societies and artificial insemination organisations.

Some play is made from time to time with the idea that unpopular breeds may be useful stores of genes. If anyone knew what genes would be useful in the future (but not now), if anyone could say whether a specific breed had them, if anyone could be nominated to undertake the task of extracting and exploiting them, the idea might have a better chance of leading to action. Although few will raise a finger to save redundant breeds, except for research, much effort has been devoted to making or introducing additional breeds. There may be a time coming when qualities such as resistance to metabolic and bacterial diseases, or efficiency of food use, may have to be rapidly developed by crossing with exotic breeds instead of by the slow process of modifying current populations.

sensible to preserve some that have become superseded as has been argued by Rowlands (1964) for wild species of animals in zoos.

Those who are interested in numerically small breeds would often like support to keep them alive, through financial assistance if necessary. A much more pertinent way in which the problem of maintaining genetic variance can be met is to subdivide large gene pools into sub-populations. Organising gene pools to which moribund breeds contribute (particularly if they are moribund on account of their small numbers and not because of their lack of merit), might be worthwhile in spite of being a highly improbable undertaking. A simpler solution would lie in banking frozen sperm, since genes stored as haploids are as useful for the purpose as those stored as diploids (see next section).

The prime issue in the whole matter is the question who is to initiate any scheme of preservation of genes or breeds, who is to direct it, who is to carry it out, and, above all, who is to pay for it. Fortunately, there is no immediate urgency in this connection, except, perhaps, for chickens. The overall philosophy of responsible decision in a capitalist society is a much more weighty matter than its application to animal breeding, and the probability is that the solution to this particular problem will have to be found from general principles. Further comments on the subject of genetic variability appear in the next chapter.

VI. Gamete Preservation

Much attention has been devoted recently to methods of preserving gametes for long periods of time. A good many of them have been found successful. Thus offspring have been produced from frozen sperm of various species of animals, frozen eggs have been successfully thawed, fertilised and in a certain percentage of cases developed into embryos following transplantation. VanDemark (in Hodgson, 1961) can be consulted for a review of the history of experimentation on this topic, beginning with the first successful artificial insemination of dogs performed by Spallanzani in the 18th century. When techniques for long range and large scale storage of frozen sperm and eggs (*in vitro* cultures may provide another way for preserving gametes) are perfected, considerable use of them might be made in livestock production and improvement. Indeed, proposals to establish extensive facilities for acquiring, preserving and distributing gametes of a variety of species have been under consideration by various agencies for some time. Although possibilities for doing so seem on the face of it to be exciting and although many purposes to which the use of such facilities could

be directed have been suggested, a sober examination of the contribution that storing gametes can make to animal improvement tends to dampen enthusiasm. Among the uses to which repositories of gametes could be put, the following may be noted.

1. *Storage of germ plasm.* This is in part a matter of regulating supply and demand. Should a type of stock be produced in excess of the needs, gametes may be saved for future expansion. Similarly, various types of germ plasm which may not have any current economic value could be stored in case they are required, and reserves of genetic variability maintained.

2. *Long range control populations* Activation of frozen gametes after many years could be undertaken to provide populations to serve as controls on the progress achieved by selection This idea requires the assumption that no gamete selection among the frozen and successfully reactivated gametes will occur. Whether this research tool would be useful for industry may be questioned. Other ways for maintaining controls can perhaps be devised at a lower cost and with greater assurance that they would serve the purpose (see the following section on control lines).

3. *Back-crossing successive generations of daughters to a single sire in order to establish highly inbred lines.* This is a likely usage of gamete preservation. But it is also likely that alternation of son × dam and sire × daughter matings would be satisfactory enough to avoid the need for long-term storage.

4. *Increasing the numbers of contemporary offspring of single individuals.* Undoubtedly, egg preservation could be of value in the progeny testing of females. However, it is probable that transplantation of ovarian segments or egg transfer could be used in a better and simpler way. For male progeny testing, more effective usage could be made of fresh semen. The only remaining possibility under this rubric is the increase in the number of offspring from progeny-tested individuals, but the considerations advanced for progeny testing also apply here.

sperm in lead-shielded containers, the number of mutations would be reduced, since exposure of gamete-producing cells in a live organism to various mutagenic agencies would be avoided. There may be some biological justification for this practice in the human species but its social, psychological and economic aspects involve controversial issues which this is no place to discuss. For livestock, the matter would appear to be of trivial significance.

7. *Maintenance and introduction of new or exotic stocks.* Transportation of gametes may be a cheaper as well as a more hygienic way than introduction of live animals. Nevertheless gamete storage for this purpose does not seem at the moment to be a particularly important technique.

Thus, while sperm and egg banks of livestock may become commonplace in some distant future, no important functions for them can be discerned at this time.

VII. The Use of Controls

The difficulties of verifying the results of selection experiments and of genetic trends in the quantitative characters of domestic animals have already been alluded to in Chapter 3. But difficult or not, operating managers of artificial insemination schemes, economic planners, and other citizens and officials need information about what genetic changes are occurring in populations of animals designed to supply food for the world. Indeed, if investigators and breeders are to provide critical interpretations of experiments, more general applications of techniques which will separate genetic from non-genetic changes is imperative, as has been argued by Goodwin, Dickerson and Lamoreux (in Kempthorne, 1960). While at first thought the cost of measurements needed to accomplish this end with livestock may seem prohibitive, more careful appraisal suggests that selection experiments without such measurements, and thus not susceptible to critical analysis, may be even more costly. The use of controls has been adopted in poultry breeding and appears to be already paying dividends to one commercial breeder employing it (Dickerson, 1962).

upon for guiding companies and institutions in making decisions on this point. It may then be suggested, if only for the sake of argument, that perhaps 10% of the estimated gain in performance converted into financial terms should be devoted to discovering whether or not an expected gain has taken place.

In the past a great deal of effort has been invested in the so-called improvement of livestock. This has been done as a matter of faith rather than on any assurance that the improvement as hoped for will actually take place. The effort of trying to estimate the cost of running control lines might even have the incidental benefit of drawing up a balance sheet which would show on the one side the costs incurred in attempting to obtain improvement and on the other side the value of the improvements achieved.

and maternal effects to be isolated (for a statistical analysis of this method, see Giesbrecht and Kempthorne, 1965). It is probably best suited to poultry where truly contemporary comparisons between sufficiently large populations are feasible.

All types of control so far devised are open to various kinds of objections, but it is to be doubted whether any of the objections are more serious, or any combination of them are more serious, than to have no controls at all. The main expense of keeping control lines, either of the independent closed population or of the repeat mating types advocated by Goodwin and his associates (*loc. cit.*), arises from the cost of maintaining a sufficiency of males, either to prevent inbreeding or to enable them to be used in successive years when they would normally be culled after one year.

In cattle, pig and sheep populations, the maintenance of control lines might be less expensive than in a poultry breeding concern where this operation has to occupy space that could be devoted to the production of chickens for sale. Recording of the necessary information and subsequent analysis are, however, major sources of expense in all animals.

The type of control adopted in any circumstances should be determined first of all by the specific questions which it is to answer, and secondly, by the permissible number that shall be available for it. This means in effect that the costs of maintaining the control animals determine their number and the volume of records made on them.

One of the complications with mammals is that maternal effects often affect the performance of repeat matings. Whenever this might happen, it would be important to have good estimates of them. One way of avoiding this complication would be to have repeated matings on the male side, either by keeping the males for several generations of breeding, or by using frozen semen. Variations of this method have been exploited by Van Vleck and Henderson (1961) for dairy cattle and by Smith (1962) who found suitable material in a pig herd for his purpose. Although valuable as a demonstration of what is possible, this method is perhaps too uncertain in operation to be acceptable as a permanent policy. It is probably only a matter of time, however, before improvements in technique will allow wider use of control lines or other methods of estimating real genetic changes, a consummation in both public and private interest.

VIII. Animal Improvement in the U.S.S.R.

Nearly all that has been so far said regarding the operational problems of animal breeding refers to the situation in the Western world. In the

Communist countries the political situation and economic structure of agriculture may make much of the previous discussion irrelevant. However, it is by no means clear what the situation is even in the Soviet Union, literature on which is abundant. The difficulties arise firstly from the rapid changes in instruction, research and development policies which seem to be unpredictable. Secondly, there is the paradox that in a monolithic state in which it is avowed that the only purpose of science is to serve the economic needs of mankind, agricultural research has, in fact, been divorced from fundamental biology.

As is well known, Lysenko was a virtual dictator with respect to agricultural genetics between 1948 and 1964. Mendelian theory and especially its statistical aspects were derided and considered to be philosophically unsound. Although Lysenko's own background was an agronomical one, he had recently turned to problems of dairy cattle improvement. His own results did not represent anything startlingly unorthodox and, even before his fall, it seemed that some of his associates were moving into the direction of ordinary population genetic approaches to animal improvement.

Since November 1964, a veritable revolution on the genetic front has occurred. Not only has Mendelism become respectable, but a drive to update textbooks and research programmes along the lines of modern molecular biology and biophysics was initiated. The great difficulty with respect to livestock genetics is the lack of informed technologists. A gap of a whole generation of genetically oriented teachers, research workers and breeders presents a formidable handicap to the prompt revival of the genetic work of the kind carried out by Serebrovsky (before Lysenko's rise to power) which in many of its features resembled that of Lush. Only the future will show how the problems discussed in this book will be tackled in the U.S.S.R.

Meanwhile, it may be instructive to give a translation of the summary of a report on the Eleventh International Congress of Genetics held at the Hague in 1963 by Lysenko's deputy director, and later acting director of his former laboratory (Kushner, 1963). Appearing, as the report did, in a belligerently anti-Mendelian journal, it gives some notion if not of the state of affairs, then at the least of the state of mind about a year before Lysenko's views fell into official disrepute.

The summary reads:

"1. The time has come to pass a special decree regarding the utilisation of heterosis in the different branches of animal husbandry analogous to the degree which in its time ensured the mass production of hybrid corn seed in this country.

"2. A systematic study of blood groups in the leading breeding populations of cattle must be organised.

"3. For a cheap mass organisation of the analysis of milk for protein content it is essential to arrange the manufacture of modern equipment and reagents similar to those widely used in Holland.

"4. It is highly desirable that feed cost in the growth and finishing of swine for pork should become a basic criterion of selection.

"5. It is necessary to commission networks of zootechnical scientific establishments which have poultry departments to create specialised strains of chickens, which upon crossing would give highly economic broilers that, at the time of slaughter (at 60–70 days of age), would expend not more than 2·5–2·6 kilograms of food per kilogram of gain.

"6. In zootechnical scientific establishments, it is necessary to broaden investigations on the problem of correlations between the most important economically useful traits of animals, so that rational selection methods for combining in the organism the most desirable traits could be worked out in different species of animals.

"7. The question of the possibility of organising studies on hereditary improvement of livestock and birds with respect to their resistance to certain dangerous diseases should be discussed by zootechnical and veterinary scientific establishments.

"8. Measures should be taken to improve the teaching of genetics in agricultural colleges and to introduce into their curricula questions of population genetics."

As the reader will recognise, the recommendations made would have been *mutatis mutandis* conservative in the West twenty years ago, albeit a good many of them still remain to be implemented. It will be of considerable interest to see whether these reforms will be introduced faster into Soviet agriculture than into Western.

CHAPTER 9

GENETIC RESEARCH

It is a main objective of animal breeding research to make these methods more efficient and more effective, which implies that this research must, in the ultimate sense, be directed towards understanding the nature of the biological phenomena underlying them. Basic research results in the public domain can benefit the world at large, whereas developmental investigations may have only local value. Furthermore, profit making industrial establishments cannot be expected to invest in excessively speculative research although public interest demands that somebody does. A whole spectrum of research projects ranging from strictly operational problems and within the ambit of industrial establishments, to fundamental biological studies likely to be undertaken only by exclusively research organisations, can be readily outlined. The limit of such a catalogue of possibilities in animal breeding research is the limit of imagination, courage and space. Carrying out the research itself is a matter of technical competence and money.

The have-not nations must conserve their resources and employ them primarily for increasing capital investment and for meeting immediate consumers' needs. Long range research which is a gamble, then must clearly fall to the have-nations In many ways both the United States and United Kingdom have risen to the challenge, albeit still at an inadequate level (see Chapter 8). But, for a reason difficult to fathom, in the socialist countries, only now does there seem to be an awakening to the need for a fundamental approach to agricultural research.

The perusal of agricultural science journals from the Soviet Union and Eastern Europe suggests that the main occupation of their experiment stations and agricultural colleges is to engage in empirical field tests without the least concern for the fundamental biological significance of the results obtained. While proper statistical analysis is being found in an increasing number of papers, proper designs are not. Furthermore, the objectives of most of the experiments reported seem to be to try something without rhyme or reason and see what happens. The alleged transformations of chickens by blood transfusion from other breeds, however, has a sort of theoretical basis in Lysenko theory, if it may be called that But experiments of irradiating chicken eggs with small doses and observing the laying performance of the birds hatched from them seem to be based on no preconceived idea of any sort. Scientific methodology presumably involves testing of hypotheses. An experiment like this does not seem to be testing any hypothesis. In the Western world also there is the risk that too many such experiments may be attempted merely because there are not enough good ideas to go around. There is, therefore, a danger that continuous spending of

public funds on trivial and pointless research will rebound and result in lowered support of science. This must not be allowed to happen. As more control of operational research is placed in the hands of commercial enterprises, it is imperative to preserve the quality of fundamental research in agriculture, including animal breeding The bigness of science is very relevant here. The growth of scientific endeavour brings in its wake an emphasis on expensive and fashionable equipment, digital computers, electron microscopes, amino acids analysers, and the like. And the costliness of experimentation with large animals makes it important to ensure that the available money and time must be spent on projects that spring from good thinking.

Lerner (1962) has reviewed a variety of research problems specific to poultry. Much of the following chapter is an extension of his article. The topics dealt with are only a sampling, and they are presented in no particular order. Although the emphasis is on basic questions, a good many topics considered have an immediate bearing on breeding practice.

environment imposed on all herds or flocks wherever they are kept, even if the environment itself is fluctuating or cycled.

Allied to this general problem is its complement. In other words, selection has until recently entailed trying to produce or find genotypes suitable for a particular environment. Emphasis could be reversed by determining the kind of particular environment, including lighting, feeding, and temperature regimes, or hormone treatments, that would be suitable for specific genotypes already in existence. If new species of animals are to be utilised in food production, this approach may be the only practical one.

On the border line between operational and basic research lies the search for highly heritable markers which might be linked with or might depend on genes controlling the phenotypic expression of economic traits. There has already been work on the determination of the levels of certain enzymes in blood or blood group as an indication of production qualities. At this stage, it does not seem clear whether the blood-grouping laboratories associated with many American poultry breeding enterprises are used for selection or have other reasons behind them, such as advertising or policing franchised dealers. Nevertheless, there are many developments in the field of immunology and biochemical polymorphism which would suggest that it may be worthwhile to continue examining blood groups, blood proteins, enzymes, metabolic breakdown products, for correlations with economic traits (see a subsequent section on biochemical and immunological variation).

Some way of circumventing the biological inefficiency of production, perpetuation and multiplication of superior genotypes is needed. It is bad enough to have sexual reproduction break up an optimal genotype because of Mendelian segregation, but added to this is the fact that production of heterotic types, dictated by the economics of the situation, is often less efficient than closed population selection. If it were possible to induce cloning or asexual reproduction, both complications of this sort would be overcome. How soon this millenium will come cannot be said at the moment, but it is the essence of an enquiring mind not to set bounds to the possible, improbable as their transgression may seem.

Much of the mathematical theory of selection and selection limits is based on simplifying assumptions many of which have already been discussed. It seems rather important to be able to verify these assumptions, and, further, to be able to remove restricting conditions. This clearly means extending biological knowledge of each species. It may be granted that general notions about the expected genetic changes

under selection which have been derived from experiments with laboratory animals can provide a partial guide to practice when larger animals are concerned. But each species has its own biology and may have peculiarities not present in the laboratory animals used in pilot studies. It is well known that under natural selection a great variety of mechanisms for attaining the same basic ends has been produced and it is hence important to find out exactly which ones have been adopted by each species. How general, for example, are segregation abnormalities in cattle, sheep and turkeys? What role does cytoplasmic inheritance or virus transmission through the cytoplasm play in chickens, swine or sheep? Is the number of alleles the same per locus in cattle as it is in bees? How important is the fact that in most domestic animals there is a large number of chromosomes instead of the few found in *Drosophila*? Is there much non-randomness in crossing-over with the consequent tendency to build up polygenic blocks? Is the estimate of mutation rate characteristic of *Drosophila* or mice applicable to pigs or beef cattle?

From what is known of genetic theory, it can be predicted that no system of selection may be expected to work efficiently for an indefinite period of time. Sooner or later (and the more efficient the system, the sooner), exhaustion of genetic variation, induction of negative genetic correlations among favoured traits, and reduction in Darwinian fitness as a correlated response, are bound to enter the picture. It is, therefore, small wonder that selection for annual egg production may after several generations lose its initial effectiveness. Reports of this have been provided by Abplanalp (1962) and Morris (1963). It is one of the great deficiencies in current breeding programmes that no signals to show when a selection or breeding system should be changed have been developed. The difficulties of measuring selection progress, owing to the great environmental variation from year to year and the costliness of maintaining adequate controls (discussed in Chapter 3), are at present too great to permit such signals, but a search for markers, or biochemical indicators of some sort, which would measure changes in the gene array from generation to generation as an index of selection progress, should undoubtedly be instituted.

that, of new genotypes and phenotypes, should be out of the question. Artificial mutagenesis is one technique that may be used to create new variation. Mutation breeding has been tried with various degrees of success in many plants. To mention only a few: barley, peanuts, soya beans, rice, potatoes, fruit trees, subterranean clover, tobacco, ornamental plants have all been subjected to radiation in order to produce variability. But the attempt, already cited, to extend this sort of study to poultry has been unsuccessful. The only project dealing with useful animals which has indications of reasonable success is one dealing with mutagenesis in the silkworm (Tazima, 1964).

Alternative methods of creating new variability include distant hybridisation which is likely after a period of selection to result in the production of new combinations. Contrary to mutation breeding, where the improvement in the genotype may be expected to occur by gene substitutions at relatively few loci, distant hybridisation may be best attempted for the production of complete novelties. Introduction of single genes from wild populations in the manner done by plant breeders is probably of limited utility in livestock. But an avenue for creating new types may lie in the selection for crossability of different species. For example, considerable variation in fertility and hatchability is found when different strains of chickens are crossed with the Japanese quail. It should be possible to select for breakdown of isolation barriers between these species and thus originate new forms of animals which might be useful for food production.

A still further possibility lies in subjecting populations to stress either by manipulating environment or by introducing foreign genes, not for their own value but for unmasking cryptic genetic variation that is present but not manifested. Examples of this approach are provided by the study of Dun and Fraser (1958) of whiskers in mice, and by Abplanalp's (1962) investigation of shock breeding in chickens.

III. Sex Control

An intriguing challenge of long standing is sex control in mammals. Many attempts of varying degrees of sense have been made to influence sex ratios at conception or birth, but so far compelling evidence for success is lacking. The most hopeful procedures are attempts to separate X- and Y-bearing sperm in the semen. Differences between them are of immunological, morphological or electrical nature. Immunological work has not so far helped much although claims for serological identification of even smaller antigenic differences than those to be expected between whole chromosomes have been advanced.

Thus, Gullbring (1957) states that the A and B blood group antigens can be distinguished in human sperm. However, Owen (in a discussion of Braden's paper, 1960) has cast considerable doubts on this interpretation of Gullbring's results, even though he thinks that the possibilities in this direction are open.

Morphological separation of the two kinds of sperm by taking advantage of the unequal amounts of chromatin in them was suggested long ago (Lush, 1925). The recent investigations along these lines are not particularly encouraging (Lindahl, 1958, 1960; Andersen and Rottensten, 1962), although some separation of rabbit X and Y sperm by differential sedimentation was reported by Bhattacharya (1962). The long standing attempts at influencing sex ratios by dietary control of pH of blood serum do not seem to very successful (Weir and Haubenstock, 1964).

Claims that there are differences in electrical charge between the X and Y kinds of sperm were first made some thirty years ago and reiterated recently on the strength of experiments with rabbit semen. They have also been criticised in a review of the evidence on the subject by Rothschild (1960). Thus, at the present time it may be said that no reliable methods of influencing sex ratios of livestock are available, but the search for dissimilarities in the two kinds of sperm, be they chemical or physical, has by no means been exhaustive and is worthwhile pursuing further with restrained optimism.

Because in birds it is the female sex that is heterogametic, similar work in the chicken, the turkey or any other species of bird, is somewhat less promising. There the mechanics of influencing sex ratio would be to identify, if possible, the X- or Y-carrying eggs, although there are no techniques for achieving this in immediate prospect. An alternative lies in the feminisation or masculinisation, as desired, of embryos whose sex has already been genetically determined. Work on the endocrinological aspects of this problem has been in progress for many years, but so far it does not seem to have led to fruitful results In fact, the only example of an useful animal in which experimental control of sex ratio has been attained is the silkworm (Astaurov, 1962 and Astaurov and Ostriakova-Varshaver, 1957). Nevertheless, the reward for solving this problem is so great that continued research, at least on a pilot scale with laboratory animals, should be encouraged.

Olsen's work with turkeys and chickens (see below), is provided by Beatty's (1957) monograph. Of the various kinds of parthenogenetic processes listed by him, those which lead to the production of diploid forms seem to be of greatest potential. There are at least three: (a) polar body fertilisation, (b) doubling of the chromosome numbers of the egg, (c) tetrad formation with subsequent reduction in chromosome numbers. Although much effort has been expended, conspicuous success in finding spontaneous or repeatably producing experimental parthenogenetic foetuses brought to term has not been achieved with mammals. Most of the treatments induce parthenogenetic development but the embryos usually do not survive.

Yet there are many techniques which appear sufficiently promising to be pursued, especially since survival in at least the early stages of life is compatible with some of these methods. Evidence suggesting the possibility of producing parthenogenetic mammals is available on many invertebrates and some lower vertebrates. In turkeys, Olsen (1960 and earlier) has found a considerable proportion of individuals of spontaneous parthenogenetic origin, as well as some conditions under which their incidence is enhanced (e.g certain virus infections of the dams). Unfortunately, in his experiments, all individuals that lived long enough to allow sex identification were found to be males. This might be expected if they arose by doubling of chromosome numbers and if X-less birds are inviable. More than twenty-five of such parthenogenetically produced males were so far found to be capable of siring offspring (Olsen, 1965). Furthermore, selection for increased incidence of parthenogenesis has been remarkably successful. Although such males are of great biological interest, it is difficult to see the other than experimental purposes for which they could be used.

It may be hoped that research on mammals in this field will be continued. Among them, it would be females that would result from a similar parthenogenetic process. And in mammals, unlike birds, practical application of a method of producing such individuals is much more promising. Rapid inbreeding, virtual self-fertilisation or cloning (depending on the nature of the apomictic process) could be practised. It has even been suggested that parthenogenetic techniques may make the male completely obsolete. Not only could females be self-propagating, but they would virtually be assured of a sort of immortality. Since no immunological incompatibility would exist between mother and daughter, a ready supply of daughters could be maintained to furnish the mother with replacements for worn-out organs.

This type of research requires the investigation of successful methods

of inducing parthenogenetic development and determination of the intra-uterine and post-natal regimens and environments in which such animals could survive. There is no doubt that the search will be a long and expensive one, but, should it be successful, some of the great problems of utilising heterosis in the larger animals would be overcome.

V. Maternal Effects

There is a great deal to be learned about maternal effects. The subject bears not only on population genetics, but also on a great many other aspects of animal production. For present purposes, a list of the types of maternal effects which need to be investigated is sufficient. Such a list will demonstrate their widespread significance:

1. *Genetic* (a) The effects of common environment of litter mates and, to a lesser degree, of non-contemporary sibs on the variance between unrelated individuals; (b) the accumulation of spontaneous mutations in oocytes of the dam as a function of her age.

2. *Cytological* (a) Cytoplasmic or plasmon inheritance; (b) chromosomal abnormalities due to irregularities of segregation in egg formation.

3. *Embryological* (a) Congenital malformation due to insults to the dam or to other causes, such as ageing and changes in the physiological or nutritional state; (b) growth of embryos *in utero* or in eggs of birds.

4. *Immunological* Mother-foetus incompatibility.

5. *Physiological* (a) The possibility of increases in the variability of metric traits of offspring due to a progressive loss of the dam's ability to maintain the proper intra-uterine environment as she grows older; (b) variation in post-natal growth of mammals as a residual of influences on the embryo or of pre-weaning nutritional effects; (c) haemodynamic and placental influences on the growth of the foetus.

offspring can be fully understood. Since so much of animal production depends on this relation, the importance of this topic of research can hardly be overestimated.

VI. Disease Resistance

There is very little doubt that Gowen's (1937) dictum that "No investigator who has adequately sought inherited host differences in disease response has failed to find them" is as valid today as when it was first pronounced. Hutt (1958) or Fredeen (1965) may be consulted for examples ranging from oysters and bees through the whole gamut of laboratory and domestic animals, illustrating the ubiquity of a genetic component in the ability to withstand disease. Although Hutt recognises that under certain circumstances other methods of checking disease may be used, he is probably the leading advocate of selection for disease resistance in farm animals At the other extreme, stand the proponents of the view that control of most diseases can be attained much more effectively by environmental rather than by genetic means

The case for selection for resistance at the expense of reducing selection pressure for other traits is very weak when diseases of nutritional origin are considered However, conversely, selection for high performance may be, in essence, selection for the correction of metabolic errors disguised as susceptibility to nutritional deficiencies.

For infectious diseases, at least in some cases, the argument is more open. Thus, until veterinarians are able to prevent or treat such a disease as leucosis in fowls more successfully than they can now, some selection for resistance may sensibly be incorporated into breeding programmes, even though no breeder has yet fully solved his problems in this way. Bacteria and viruses can, no doubt, evolve faster than chickens or cattle, and reliance on resistant genotypes to keep livestock free from disease is weak insurance. It appears that much of livestock production is now moving towards disease-free environments Both gnotobiotic (germ-free) as well as specific-pathogen free herds of swine have already been made available (Trexler, 1960, see also Pollard's 1964, article on the use of gnotobiotes in biological research, and Luckey's 1963 book). Indeed, Ross (1960) has computed that 20 million head of hogs of this type could be produced by 1967 in the United States. Whether or not this would be economically sound is another matter, but it does seem that before long, disease-free farming will be possible technically, at least, for swine and for chickens.

Interdisciplinary research on this subject is called for and the cooperation of pathologists and immunologists is vital, but there is a long tradition of geneticists approaching it on their own. The line between geneticists and immunologists is growing very thin, and it hardly matters in which section of this chapter the matter is brought up. But it should be kept in mind that the whole issue of disease control by genetic or environmental means is rendered exceedingly thorny, not only by its relation to animal improvement but also because in it the safeguarding of public health is at stake.

VII. Biochemical and Immunological Variation

Biochemical variation in livestock involves at least three related topics: (a) intra-specific serological differences in red blood cell antigens; (b) histo-compatibility antigens, (c) serum, albumen and enzymatic variants.

For the first of these, there have been recent literature reviews by Stormont (1958), Briles (1960), Rendel (1961) and Gilmour (1962). In addition, a comprehensive investigation of the relationship of blood groups and production traits of dairy cattle has been made by Neimann-Sørensen and Robertson (1961). The basic facts which hold for all species are:

1. Polymorphism (existence of genetic variants in a population at levels that cannot be accounted for by recurrent mutation) is common.

2. Inbreeding does not seem to lead to the expected increase in degrees of fixation at many of these loci.

3. In some instances, non-inbred populations have more heterozygotes than expected from Hardy-Weinberg equilibrium frequencies

4. In spite of these facts, no compelling evidence for a strong association between fitness or production characters on the one hand, and genotypes for blood group antigens on the other, has been produced either in cattle or in sheep (Stansfield *et al.*, 1961). Chickens are a possible exception, though in them the situation does not seem to be quite clear (see for instance Morton *et al.*,1965).

The problem, naturally, arises as to what the circumstances are that maintain this extensive polymorphism, since it seems unlikely that blood-groups which have succeeded in perpetuating themselves at a high frequency in a population would prove to have very detrimental effects on any character for which livestock had been strongly selected

over many generations. This question is not only relevant to domestic animals, but also to many other species, including man. Although various selective mechanisms, involving either heterozygous advantage or fluctuating advantage of one or another of the homozygotes depending on age or on environment (in particular, exposure to disease-producing agents of various kinds), have been suggested, the field may be considered to be an open one deserving further close study.

Whether any of the useful domestic animals, except the chicken, is suitable for pursuing generalised investigations on this subject may be open to doubt. Yet, because of the widespread practice of blood-typing of cattle for other purposes, attempts to link the data thus obtained with information on fitness or productivity should certainly be fostered.

Polymorphisms at histocompatibility loci raise many important biological problems going much beyond the bounds of this discussion. In the realm of livestock improvement, some studies are only in their initial stages as is the investigation of Schierman and Nordskog (1961) on the relationship of blood groups to transplantation antigens in chickens (now confirmed by Craig and McDermid, 1963). The value of this kind of research may be greater than that of other polymorphisms, since full understanding of ways of bypassing immune reactions can lead to successful organ transplantation

This technique is of great interest from the standpoint of therapeutics and rejuvenation, and, even more so, when specifically used for genetic improvement. Small sections of ovaries from superior dams could be transplanted to any number of potential foster mothers after their own ovaries had been removed or destroyed so that they could serve as incubators This would permit a great number of descendants of a single female to be produced. In chickens, perhaps one thousand to two thousand offspring of a single hen could be obtained in a short period of time. The recent advances in immunology imply that projects of this sort are by no means visionary, although many procedural difficulties remain to be overcome.

Polymorphisms have been observed in serum proteins, egg proteins and in various enzymes. Development of the technically simple but powerful methods of electrophoresis has led to a blossoming of studies of genetic differences between and within species. The comprehensive review by Ogden (1961) on biochemical individuality of larger animals mentions a great many polymorphisms in protein composition. Particularly numerous are haemoglobin variants in cattle. In some other species of domestic animals, different types of haemoglobin exist (adult and foetal) but they are usually present in all animals and,

therefore, do not belong to the class of polymorphs. A recent report by Manwell *et al.* (1963) suggests that control genes for switching off production of early embryonic haemoglobin may not be the same in bantams as in the larger breeds of fowl.

Among other serum proteins, the transferrins show many polymorphisms in cattle, sheep. pigs and goats. A suggestion has been made by Ashton, Fallon and Sutherland (1964), that there is a relationship between genotype for this serum constituent and some useful traits in dairy cows although Datta *et al.* (1965) were not able to confirm this fully. More recently, genetic differences in serum transferrins of chickens have also been found by Ogden *et al.* (1963).

In the proteins appearing in milk and eggs, there also seem to be distinct polymorphisms. The different types of β-lactoglobulins of cows' milk are controlled by genes with frequencies varying from breed to breed (see Ogden's review, *loc. cit.*). In chicken eggs, independent studies by I. E. Lush (1961) and by Feeney *et al.* (1963), utilising starch-gel electrophoresis, indicate that there are genetic variants in the kinds of protein constituents a hen secretes in the production of egg albumen. Evidence for linkage of egg protein loci (Buvenendran, 1964), as well as of genes controlling casein variants in cows' milk (Grosclaude *et al.*, 1964, and King *et al.*, 1965) has been produced.

Finally, genetic variability in such enzymes as catalase, esterases and phosphatase have been reported in dogs, rabbits, cattle and pigs (Ogden, *loc. cit.*), in mice (Petras, 1963), and in chickens (Wilcox, Van Vleck and Shaffner, 1962). In chickens it has also been reported that there is corresponding variation in egg production. If this finding is confirmed, selection on the basis of the serum alkaline phosphatase of young birds might be useful in attempts to improve egg production.

In the light of current discoveries in molecular biology confirming the fact that genes are essentially determinants of protein structure, it is not surprising to find so many genetic biochemical markers distinguishing individuals within a species. In human beings, it is known that certain physical and mental properties are associated with biochemical departures from the normal. Common examples of this are phenylketonuria, galactosemia, and a great number of other inborn errors of metabolism (Harris, 1959), some of which can be corrected when identified early in life by providing proper environment. The important problem which concerns a geneticist dealing with stock improvement lies, firstly, in explaining how variants of this kind come to be maintained in relatively inbred populations (a concern he shares with the student of evolution), and, secondly, in attempting to harness them for livestock improvement.

Contrariwise (N. Inouye, unpublished) tried in vain to make homozygous an X-ray induced and cytologically identifiable translocation (also in chickens).

IX. Euphenics and Genetical Engineering

In the past, it has been often debated whether nature or nurture, the genotype or the environment, was the more important in shaping the phenotype. Today the argument is no longer a matter of subjective opinion, but can be readily solved in plants and animals (though not so easily in man) by experimental determination of the degree of heritability. Hence it is possible to make reasonably intelligent guesses as to how much improvement is to be expected from changing the average genotype of a population by selection (for a theory of selection limits, see Robertson, 1960, and the discussion in Chapter 4).

It is certain that much more is to be learned about improvement of performance by changing the environment. Only relatively recently the discovery was made that feeding antibiotics increases growth rate was made. The last word has probably not been said on such topics as vitamins or trace elements, optimal lighting or temperature regimens for different animals, and sub-clinical infections; but it is clear that in the future, improvement of genotype and environment must go hand in hand. A changed genotype may perform better in a changed environment, and a changed environment may call for selection to change the genotype.

Beyond these tried and tested methods of increasing food production, recent developments in molecular biology open vistas of still other techniques to make the most of our animal resources. These are Lederberg's (1964) euphenics, and, what Tatum (1964) calls genetical engineering.

Euphenics by analogy with eugenics refers to the improvement of phenotypes based on defective genetic constitutions. For example, in man there is an inherited metabolic error leading to the disease phenylketonuria It is caused by the inability of the liver to produce an enzyme needed in the conversion of the amino acid phenylalanine into tyrosine. This block causes phenylalanine and phenylpyruvic acid to accumulate in the blood stream and in various tissues including the central nervous system. These substances have toxic effects and produce a variety of unpleasant symptoms, including severe mental retardation. Euphenic correction of the disease might be brought about by transforming liver cells by treatment with genetic material (DNA), that includes instructions how to manufacture the missing enzyme. Transformation of

this kind has been achieved in tissue culture, and it is probably only a matter of time before it can be accomplished *in vivo*.

Naturally, the first application of euphenic measures, except for preliminary experiments, would be in man. Indeed, the costs of applying this idea to domestic animals may forever remain prohibitive, but the possibilities of transformation, grafts, organ transplants, and other corrective methods should be kept in mind.

More remote in time, but probably much more applicable to domestic animals, is genetical engineering, that is, artificial manipulation of the chemical information which determines the phenotypes of the generations to be produced. Here there would be only the initial cost: once a change is induced, the information will continue to be passed on to successive generations through the germ cells. In Tatum's (1964) opinion, there are three important aspects of the subject of which man would need to acquire mastery in order to make genetical engineering more than a dream. The first of these is control of mutational processes. The second is the development of methods of designing or synthesising the genetic determinants, be they similar to the classical concepts of the gene or of some other nature. The third is the perfection of methods of introducing into living systems genetic determinants tailored to order.

As in Lederberg's vision of euphenics, Tatum's concern was primarily with human beings. However, before this stage is reached, a similar approach to animals will have been accomplished. It may be debatable whether or not centuries or merely decades will provide enough time for biologists to accomplish the feats which genetical engineering of this precision would require. There may be some doubting Thomases to question whether the goal is attainable at all. Be that as it may, it would be foolish to be dogmatic to the point of denying the possibility of these and even more startling innovations.

If directed mutations or even beneficial artificial mutations, which are not directed, become available to technicians in animal breeding, a vast array of new genotypes of livestock will emerge. Similarly, if genetic determinants can be manufactured synthetically, and then introduced into the germ cells or early zygotes, completely novel phenotypes will be obtained. Genetical engineering, distant as it may seem, would make much of what has been said in this book obsolete; but it would also go a long way towards solving the many problems that have been discussed.

X. Interdisciplinary Studies

Most research projects require the combined efforts of various specialists, and would be unlikely to be solved soon by specialists in genetics

Of less immediate practical interest is the biochemistry of inter-specific differences. However, this subject provides such a radical departure from the classical methods of studying the genetics of higher organisms that it is one of the most exciting and interesting new fields of evolutionary studies. In the past, genetic investigations could be carried out only on animals which interbreed. It is true that attempts at phylogenetic reconstructions have been made on the basis of degree of similarity in morphological, physiological or immunological traits of different species, but the newer techniques present opportunities undreamed of only a few years ago. One step in this development lay in discovering the procedures for identifying amino acid sequences in the structure of various proteins ("finger-printing"). Ingram's (1963) extensive work on haemoglobins provides a good example. Studies on various proteins in different species, including comparison of the structures of adreno-corticotrophin, insulin, cytochrome-*c*, and many others have already been carried out (for a recent study involving lactic dehydrogenase, see Wilson *et al.*, 1964).

This type of information is superimposed on knowledge of the manner in which the amino acid sequences are determined by codons, which are the intra-genic units that instruct the cellular apparatus what amino acid is to occupy a given place in a protein chain (see Woese, 1963, and Lanni, 1964, for reviews of "genetic coding"). As a result, it becomes feasible to determine the number of mutational steps which have occurred in the course of differentiation of species from a common distant ancestor. Essentially this amounts to the study of the genetics of non-interbreeding animals. Probable phylogenies of different species can be constructed, and the historical past thereby illuminated. To a scientist it feels aesthetically and intellectually satisfying to learn the likely steps by which horse and human haemoglobin diverged in the evolutionary past. It is a great achievement to be able to establish with some certainty the origin of man from African rather than Asian ancestors. In due time, perhaps full understanding of the relationships among domestic or potentially domestic species of animals may help in some way in food production. From the standpoint of adding knowledge to our insight of evolution, these biochemical discoveries have already proved exceedingly valuable. Their use in animal breeding is, for the time being, not easy to foresee, but Faraday's classical riposte, "what use is a new-born baby?", comes to mind. To acquire knowledge for knowledge's sake is a compulsion for human beings. The problem, however, in defining the functions of organisations specifically set up to study animal breeding is to justify why they should be charged with a given kind of research. More attention to molecular biology should

probably be paid in animal breeding and animal husbandry departments. It is clear, however, that if they were organised on a substantial scale to do so, they would have to compete for staff and facilities with other units which are devoted to fundamental research. Peaceful coexistence suggests itself, but there may not be enough first-class talent to go around and this may prove to be the limiting factor in the advancement of basic knowledge in animal breeding.

VIII. Cytogenetics

Attention should be drawn to the recent rekindling of interest in mammalian cytology. With the invention of new methods for chromosome study, the discovery of sex chromatin, the identification of the Y-chromosome as the sex-determining factor in mammals, the accumulation of many instances of defects and diseases produced by chromosome abnormalities, the hypothesis regarding inactivation of one of the sex chromosomes in somatic tissues of female mammals, and with many other stirring developments, the field of cytology has become exceedingly active. Not only have clinicians become greatly interested in it, but also students of evolution, who have once more started investigations of the phylogenetic relationships of primates and other higher organisms from chromosomal evidence. So far, activity of this sort in domestic animals is limited, but the field is one worthy of fresh attack, especially since it is one in which the researcher escapes from the limitation of long inter generation intervals on the rate of scientific advance. The reviews by Chu (1963) and Welshons (1963) are recommended as an entry to the literature on this subject.

Some excitement in human genetics has been caused by the discovery of variation in chromosome number and its connection with various human disorders of mind and body. There can be little doubt that chromosomal aberrations, similar to those found in man, occur in domestic mammals, and possibly, birds. It seems to be a fertile field for fundamental investigation, since experimental breeding in them is feasible, whereas in man it is not. Healthy animals that are homozygous for translocations are conceivable. Should these become a reality, copyrighted stocks of hybrids produced from crosses of homozygotes for the standard and the translocated arrangements, respectively, could become an exceedingly important item in stock production, because it would be impossible to breed from them. One apparently successful attempt at making a translocation homozygous in chickens (Bernier, 1960) has been reported, although unfortunately this spontaneous translocation studied could not be seen under a microscope.

working alone. To conclude this chapter, some very broad cooperative efforts between different disciplines will be referred to, merely as an indication of the potential in breeding research opened up by modern biology. The opportunities here are so numerous that only a few can be mentioned and even these without details.

The vital problem of the nature of heterosis requires the collaboration of enzymologists and geneticists. If it is assumed that proteins and especially enzymes are responsible for rates of biological processes and their buffering, it seems reasonable to expect that the investigation of the major enzymes found in hybrids could throw light on the physiology of this obviously important aspect of animal production.

The fields of embryology and developmental genetics have not yet contributed extensively to the much needed synthesis between them and population genetics, at least as far as animal breeding is concerned. Yet there are many exciting and challenging ideas in the marketplace of these disciplines which show promise of developing. So far, biological aspects of such concepts as redundancy, developmental noise, and canalisation (see the section on information theory in Chapter 10), are far from practical animal production. But at least an attempt to disrupt canalisation (equivalent to experiments of Dun and Fraser, 1958, which involved changing the background of a gene to unmask cryptic variation) is planned for sheep (S. S. Y. Young, personal communication).

Physiology of growth, physiology of reproduction, and physiology at large also promise an important contribution to the amelioration of animals. Not only is understanding of the elements of many basic processes that enter the production of useful foodstuffs and fibre deficient, but even at the purely empirical level, little is known about the optimum way of handling animals Circadian rhythms have not been studied in large domestic animals. Is cycled environment a necessity for efficient production of meat, eggs, milk or wool? Joint studies on the larger animals should lead to answers to such questions.

improvement of animals is obvious. No matter what has been said earlier regarding disease resistance, should specific bases for the ability of organisms to withstand invasion or damage by pathogens be discovered, it is clear that such knowledge could be put to useful ends by breeders.

Psychologists and ethologists could combine with geneticists in the study of animal behaviour. Indeed, behaviour genetics is becoming an exceedingly important field in the eyes of psychologists. From the standpoint of animal breeding, very little exploration has been carried out. And yet such questions as the genetic basis of docility, the peck order in birds and mammals, the relationships between twins, the influence of social contacts on performance, will have a significant bearing on the level of production that can be obtained by suitable management.

The catalogue of projects of this type could be made interminable. But enough examples have been given in this chapter to show how vast the arena of research yet to be done is.

CHAPTER 10

INFORMATION AND DECISION

The ability of an organisation or farm business to succeed by adapting itself to changes, or by taking advantage of them, lies in the hands of its management. Although a manager is commonly thought of as a doer, in modern management decision-making is his main function. The pace of events now means that wrong decisions can have disagreeable consequences very quickly, and management cannot afford costly trial and error methods.

In recent years statisticians and experts in business administration have been increasingly preoccupied with a quantitative approach to decision-making. Not only highly intricate mathematics, information theory, and the statistical theory of gains, but philosophy, sociology, and psychology also enter into the complex discipline which is evolving. All this is highly relevant to animal breeding. Population genetics aims to set out the rules of variation in populations but it does not set them out to the last detail, nor, indeed, to the last significant detail. Its very comprehensiveness and power to accommodate any regular forces controlling the segregation or multiplication of genes makes it unsuitable for coping with the behaviour of individuals. The same difficulty obstructs those who would apply decision theory to the practice of law, probably the most ancient decision-making institution. While geneticists generalise, lawyers, and judges try to deal with specific cases in a specific manner (Cowan, 1963).

The processes of arriving at decisions therefore vary from law to politics to science. The originally gradual, and lately rapid, metamorphosis of scientists from being observers of nature to being decision-makers on a national scale has created a need for lawyers and politicians

instance, those dealing with ducks, geese, rabbits or goats, may still contribute substantially to the agricultural economics of some under-developed nations, but they have little place in an industrialised society.

II. Profits and Values

How is the success of a breeding enterprise to be judged? As Churchman (1961) says, the idea of maximising profits in private enterprises is too vague. If it is enquired *when* they are to reach a maximum, the uncertainties arise at once. The goal of immediate profits rules out research and investment for the future. At the other end of the time range, there is horizon planning, that is, planning specifically for the point in the future beyond which no useful information is available. The concept of horizon, however, in essence begs the question, since creating information, and hence defining where the horizon is, must be part of the plan itself. Difficulties would arise for breeding establishments in both types of planning, especially when dealing with long-lived animals. Rapid genetic gains by a competitor who abandons long range goals may prove financially fatal to a horizon planner. Yet it is essential to carry on long term development and operational research in view of the need to raise national productivity, and to cope with changes in markets and husbandry. Among these, secular changes in the environment of herds and flocks, hitherto inexperienced diseases, unpredictable climatic variation, new developments in food processing and merchandising, changes in consumer preferences, and many others come to mind. One of the reasons for the integration in agriculture lies in the need for maximising controls over the direction in which some of these factors move In the poultry industry, for example, the breeding programmes as well as production operations with birds laying brown eggs, would probably have been cushioned against the economic set-back they experienced in California had they been under the control of the groups which developed the highly efficient apparatus for candling only white eggs

Most pedigree herd owners in practice fix their horizon near at hand, for the good reasons that they can neither see ahead very far nor wait long for profits For larger private enterprises, such as poultry firms or artificial insemination concerns, the problem of allocating current resources to genetic research and development seems to have no logical solution. Profit and loss accounts say nothing about neglected opportunities for securing new markets, or breeding better strains, and overhead costs cannot be related to any objective measure of efficiency or

skill in organisation. A business which does not strike a satisfactory compromise in the conflict between long and short term considerations will sooner or later be at a disadvantage in a competitive economy.

Troublesome as the problem is for a large private concern, it is more complex still for a public institution such as the English Milk Marketing Board. Are the rules for its administration the same as for a private business? How much should it spend on research? Should it follow policies favoured by its constituents, or government policies? Should it encourage or try to destroy competitors? Should it try to make a large profit, a small profit, or no profit? Is it expected to help uneconomic small scale farmers, and ailing breed societies? What kinds of cattle ought it to select and breed for? Are its interests to be limited to dairying, to agriculture, to Britain, to Europe, or to the world? Each of these questions is political, but each has a scientific undertone.

III. Information

Decision-makers will have much information on which to base their decisions, but they will still be required to exercise foresight and judgment. This applies as much to those who are operating public or semi-public artificial insemination schemes, as to the managers of poultry enterprises. More efficient methods will lead to a faster rate of change, but it does not follow that the direction will be permanently correct. However, as more information about markets and production becomes available, the risk of persisting in wrong policies should in fact be progressively reduced. Yet, since economic and agricultural statistics have an authoritative air about them, it is well to remember that they often suffer from three defects. They may refer to a relatively distant past and therefore be irrelevant to some degree; where based on estimates or samples, they can be inaccurate; and, owing to varying assumptions and meanings, they can mislead if used for comparisons between countries or regions. In rapidly changing circumstances, statistics open to any of these criticisms will not be helpful, with or without a computer.

Since decision-makers cannot know of all current and future events that would influence them, some selection of data has to be made. It is a reasonable guess that, had different selections been made in the past, decisions would also have been different. Facts available are often those which have been collected for some other purpose, and subject to various biases that may have been irrelevant to the original purposes. If, instead of being based on lactation milk yields because there is an apparatus for collecting them, dairy bull selection had been based on

to understand not only how they arrive at decisions themselves but also how scientists arrive at them. It is up to scientists to study and understand the workings of their own minds and to make them clear to others.

In a political democracy, it is impracticable for everyone to take part in decision-making except on the largest and most general issues. Where governmental decisions are needed in technical matters, they are made by a few people who are supposed to be armed with all the relevant information and the ability to use it properly to come to decisions. As far as animal breeding is concerned, and it is a large industry, this "intelligent layman" technique manifestly does not work.

In this field it sometimes happens that the decision-maker somehow decides what he wants and then supposes it is the duty of the scientist to tell him how to get it. A significant part of management, however, consists in trying to find out what results are wanted, and the scientist is thus put in the position of having to suggest what decisions ought to be taken. This leaves the decision-maker with the task of dealing with incomplete data and of taking the risks. Furthermore many decisions arrived at on the basis of scientific counsel given in one situation may have entirely unforeseen consequences when implemented in a changed situation of which the advisors are not apprised.

In animal breeding it is now impossible for those unfamiliar with genetic science to criticise its assertions after only brief consideration, no matter how penetratingly intelligent they may be. If advantage is to be taken of genetics, some reliance must be placed in its principles and chief exponents. Churchman (1961), in a different connection, puts the matter as follows: "The true 'facts' are the assertions accepted by a few whom our society trusts. As a culture we tend to trust our physical scientists, and tend not to trust our social scientists. We trust no one if we can see the direct relevance of his assertions to changes in our national policy and our personal lives." Although the difference between the policy-maker, the administrator, and the scientist may well disappear in a future blessed with an accepted science of values, the present seems to be characterised by distrust.

I. Types of Enterprise

There is little doubt that what the future promises is integration not only within animal breeding but embracing food production and distribution. The paths by which the eventual structure of agriculture

is reached are uncertain but at least four levels of integration may be visualised:

1. The breeding, manufacture and distribution of the products of a single species.

2. Breeding operations involving different species but independent of production and distribution.

3. International co-ordination with a single company or an inter-locking organisation controlling the breeding of a given species in different countries.

4. Complete integration of all processes of animal food production from breeder to retailer covering all species, and internationally organised.

The highest level depends on political and economic relationships among nations and is unlikely to develop in the immediate future. Meanwhile, although no complete monopolies have developed within the other three stages, a trend towards them may be discerned and it has naturally increased the amplitude of decision-making in animal breeding.

Decisions by governments regarding prices or subsidies for agricultural products, or research, or marketing and development boards, can change the fortunes of breeds very suddenly. Then there are actions leading to the growth of business empires with incidental effects on breeding and breeders. At the other extreme are the decisions by some individual breeders to do nothing to adapt themselves to changed circumstances and so to acquiesce by default in the changes which will make them redundant as breeders.

Viewed from the standpoint of control and decision-making, there are four categories of enterprises in animal breeding.

1. Completely nationalised industries like those in communist countries.

2. Quasi-governmental organisations depending on economists, scientists and technicians for management on behalf of farmers or farmer co-operatives. The Milk Marketing Board of England and Wales is an example.

3. Individuals or corporations employing professional managers to operate the business for profit. American Breeders Service, Curtis Candy Company, and Kimber Farms in the United States, and the Ross group in Britain are cases in point.

4. Unorganised small scale private enterprises. As a class this category has rather poor prospects in industrialised countries, except in minor types of food production not worthwhile nor easy to organise (such as bee-keeping). Many such undertakings, for

body weight, cow populations might now have been different and perhaps superior. If breed societies had fully recognised the value of artificial breeding as an aid to progeny testing, they might have tried harder to exploit it from the beginning. Once decisions have been taken and effects produced, there can be no return to the original position. They can be reversed but the new decisions now apply to a changed population of animals and farmers in new circumstances.

Data cost money and there must inevitably be a tendency to make do with the cheapest or dispense with them altogether. What information to collect and how much of it are two of the first questions to be answered by operational research. Even when the answers are available, however, their value is short-lived. To be influential, therefore, statistics and performance records of all kinds must be available when the moment for making decisions is at hand. Speed must be allied with accuracy and relevance.

Animal breeding can never be the same as it was before the computer. Data handling that would require an inconvenient army of clerks is now necessary in the poultry and dairy cattle organisations, and will be necessary for the pig and sheep organisations of the future. In any conflict of views, information is a powerful weapon and it is in the hands that control the computer.

Information is not just a question of market intelligence or prompt reports of progeny tests It includes a constant weighing of alternative products and procedures and an awareness of the results of research. Communication, however, even among scientists now verges on anarchy (Coblans in Goldsmith and MacKay, 1964), and for others interested in research findings, the position is worse. At its best, it has been likened to wind-pollination. In some ways, the process of making known the results of research appears extravagant and wasteful, as is the process of getting the results in the first place Many workers and papers of no great significance have to be accepted in order to make sure of obtaining the few that are important. Van Vleck and Henderson (1965), who incidentally provide an admirable discussion of the use of statistics in reports of experiments related to animal production, think that negative results should be even more widely publicized to help in the planning of research

Publication in a scientific journal serves three purposes: those of the author, the reader of current issues, and the future inquirer for recorded facts and hypotheses. Although these conflicting interests have not yet been reconciled, the spate of literature is forcing some changes. Coblans (*loc cit.*) considers that it is gradually bringing nearer to realisation proposals made from time to time that short pithy resumes

be widely distributed, while long papers with data be centrally stored and be available on film for those who need detail.

Some such separation will have to be achieved for decision-makers if they are to have time to expose themselves to new ideas and put them promptly into action. Meantime, the gulf between research and its application tends to widen for those managements which cannot or do not wish to keep in touch with research. This has happened with animal genetics, except where enterprises are large enough to support the employment of geneticists.

the desired ones or on the phenotypes of related animals. Noise, in this instance, is produced by environmental effects which tend to obscure the real genotype of the animals. There is an important relationship between these concepts. To quote King: "Just as the ratio of amount of information in a message to the minimum necessary to express it determines the redundancy, the ratio between the amount of information sent and the amount received determines the 'equivocation', the amount lost because of noise. Therefore, for a given message transmitted over a given channel, whenever redundancy is greater than the equivocation, the probability will be high that the message received will be accurate."

Now, to provide the necessary amount of redundancy and to minimise noise, costs time, labour and, of course, money. The numbers of measurements on individuals and on their relatives that could be made is, naturally, unlimited. The question is which measurements permit the most accurate evaluation of the genotypes when the costs of increases in accuracy of the message relative to the amount of extra gains obtained are taken into account.

Thus the application of information theory to selection would require, among other things, the determination of the most economical levels of excess of redundancy over equivocation. This is equally true of the methods of the old-fashioned breeders, whose evaluation of economic merit may have been based on the examination of individuals for pedigree, or for breed, or on individual type points, or on type as an unquantified entity, and of the elaborate selection indexes which call for measurement of a great number of traits

In the first case, instead of redundancy, it may be noise which is being added by extra measurements or impressions which the breeder uses in selection In the second, the required redundancy may be too costly for the degree of accuracy which can be obtained, especially if an index, despite its comprehensiveness, fails to lead to genetic improvement in a population. Conversely it is also possible that the genetic theory of selection indexes may in fact produce low equivocation but may be failing to keep redundancy at the optimal level

There is no doubt that not only selection but many other points involved in the organisation, theory and practice of animal improvement could also benefit from drawing on information theory. It may be hoped that it is only a matter of time, and not a long time, before extensive use of the considerable arsenal of techniques available to the experts in this subject will be introduced into animal breeding.

V. Cybernetics

Cybernetics, or the science of communication and control, has in recent years begun to pervade biology. At the molecular level, modern theories of gene action are based on the existence of intra-cellular self-regulatory devices (Jacob and Monod, 1961). The development of individual organisms has similarly been treated in cybernetic terms (Waddington, 1957). And on the population level, organic evolution itself has been viewed as a feedback process between genotype and phenotype, and between phenotype and environment (Schmalhausen, 1960). For a comprehensive review of the subject, Ashby (1956), as well as Norbert Wiener's original work (1948), should be consulted.

The idea is applicable to domestic populations of animals and the the manipulation of the contents of their gene pools by man. Essentially, whether breeders realise it or not, feedback processes of various kinds have been continually dominating their operations. For example, when selection for increased fat in pigs was so successful as to make lard a drug on the market (there were, of course, other reasons than successful selection), the feedback to the breeder led him to reverse the goals of selection in the direction of leanness

A more automatic process of this type can occur when selection for some trait carries in its wake reduction in fitness and thus puts a brake on further gains in the desired character (see section on correlated responses, in Chapter 4). Thus, selection for size and conformation of turkeys was accompanied by loss of fertility.

Effective breeding programmes depend on feeding genetic and economic parameters into calculating machines or computers in order to work out selection indexes or other selection criteria. But (as noted in Chapter 4) every time that there is response to selection, the values of these parameters change. Re-evaluation has then to be undertaken at frequent intervals. In time, no doubt, a fully automated circuit will make such adjustments without specific instructions at each step. It is interesting to speculate whether or not the lag between selection and marketing of a product, which in large animals must occupy a considerable period of time, will prevent such automatic procedures from becoming useful.

A single breeding establishment responsible for propagating not one but many species of animals may be common in the future. Cybernetic connections between all of the breeding programmes under the control of such an establishment will have to be made. And here it is perhaps the economic parameters that would play a more important role than the biological ones A breeder who has a virtual monopoly of the improvement of both turkey and chicken broilers may find that he is competing with himself. He may therefore have to shift the emphasis in his selection programmes so as to make an economic differentiation between the two species under his control.

It may be a long time before economic planning of livestock production on a nation-wide basis is introduced in free enterprise countries Indeed, it appears that even in socialist states decentralisation of planning is being tried. Nevertheless, since such questions as the number of cattle or the number of broilers or turkeys that would meet the foreseeable demands will need to be answered, linear programming for arriving at an optimum structure of the breeding industry will have to be introduced, if only as a guide-line for private entrepreneurs. The computing services for working out maximum profit plans for individual farmers, which are already available, would merely have to be expanded on, first a regional, later national, and perhaps eventually, world-wide basis The complications of horizon-planning would be greatly magnified but there is nothing intrinsically improbable about this kind of future.

As with many other topics considered in this book, only a passing reference, to cybernetics can be made. It takes, however, but little imagination to extend the ideas both to broader areas and to more specific points than has been done here. There is little doubt that cybernetic theory, like information theory, is destined to play an increasingly important role, not only in research, but also in commercial production based on animal breeding.

VI. Decision Theory

Mathematical and statistical tools for evaluating courses of action are now being brought together under the label of decision theory. It is really not a single theory but a collection of techniques for weighting numerous factors in a logical and systematic fashion. Where all the factors are known and predictable, decisions are made with certainty. Other methods, such as linear programming, cope with cases where there are chances that can be accurately measured or calculated or where there are only uncertainties. These are merely aids for there is no way to be sure of coming to the right decision. Such questions as the highest safe stocking rate, the best breed or cross to use, and the best ratio of crops to stock, are not capable of exact answers for any one farmer, nor for all farmers. Assumed biological constraints of density-dependent character are out of date for the most part. Furthermore, economic conditions change, and farmers vary in skill, energy and resources. The newer aids to decison-making are intended to be an advance on intuition and rule of thumb but carry no guarantee of correctness.

According to Alfandary-Alexander (1965), who has discussed this subject in general terms, one of the most useful services a decision-theorist can perform is to list alternative courses of action and spell out the consequences associated with each. He might also encourage preliminary trials or samplings so that as in classical statistical theory, probabilities based on experience can be used.

The choice of one or other of the various criteria is a matter of temperament: pessimists favour one kind and optimists another. What the decision maker may do after he has made his decision to prejudice the chances of his being right is, doubtless, also a personal trait.

Decision-makers who are bad losers can attempt to minimise the regret experienced after results are known The amount of regret would be measured by the difference between the actual results and what might have been had the future been accurately foreseen. To minimise regret they should choose that course of action which has the minimum of all the maximum regrets. This criterion is called minimax regret. For executives with more sanguine temperaments, there are other ways of approaching decisions.

are now looking for more effective ways to integrate expert judgment and mathematics. They want to take full advantage of the comprehensiveness of the human mind to augment the analysis. Something might then be done to encourage probing or sampling the environment in order to get better estimates of the conditions likely to prevail. Managers or decision-makers, in whatever occupation, will from now on neglect to apply analytical methods to their operations only at their own risk. For the foreseeable future, however, they have no reason to fear that they will be completely replaced by machines producing decisions untouched by human brains.

Those responsible for livestock breeding enterprises will find a relevant process in the ramifications of the screening by which superior animals are found and multiplied. Given a predetermined outlay on facilities and resources for testing (an assumption which by passes a major problem), the disposal of these resources in the most effective way makes a complex study. Robertson (1957) and Skjervold and Langholz (1964a) among others, have made important contributions to the specific problem of testing artificial insemination sires, King (1955) to the use of pig testing stations, and Young (1961) and others, to the general theory. These are examples from the greater field that includes the search for new varieties of plants, drugs, antibiotics and herbicides. Federer (1963) has briefly reviewed the subject and lists over 500 references The fundamental question in this whole area is one that artificial insemination sire testers are well acquainted with: at what point in the progression of testing, terminating the test, and starting a new test will the expected gain be at a maximum? Finney (1958) opened up the subject of the relationship between the resources allocated to the screening process and the importance to the national economy of the improvements thereby obtained. If today there is any correlation here, it might well be coincidental. To discover how decisions about resources came to be made would require much research. It is virtually certain, however, that they were not based on a careful calculation of expected benefits. Yet there must be a theoretical optimum amount of effort distributed in an optimum way among the several stages of selection It will depend in part upon the relative importance of the animal, and in part on the cost in time and money of each extension of the testing programme For the larger livestock, a clarification of this topic is called for, but meantime it is worth remembering that any scheme for the selection, testing and approval of new varieties which proceeds too cautiously, can be a handicap if the breeding programme on which it is based is to be effective.

VII. Farmers as Decision-makers

Farmers as a class include some who are able to manage large enterprises. At this stage of history, a sifting is taking place. A few will succeed in organising big units. They are unlikely to be those who are constitutionally incapable of appreciating the opportunity science creates or of providing attractive work for the technologists who could serve them. The class known as scientists also contain a proportion temperamentally able to harness skill and energy in the building up of large production and marketing organisations. Farmers' unions and co-operatives are wise to recognise that the ability which makes a good research worker depends in part on brains and resourcefulness in the face of variations and obstacles, qualities that have their value in other occupations.

In all the recent history of animal breeding, covering a period of flux in methods and objectives, it is not easy to think of any example, in any country, of organised pedigree breeding in the forefront of developments now obvious to all. This was to be anticipated since all evolution proceeds at a variable pace. Advances lead to periods of comparative stability while forces are marshalled for further progress. Bureaucracies, whether of breed associations, research administration or government, are the marks and the symbols of those temporary ends. Reformers have to remember that the rapid rate of change now means that a new and apparently forward looking institution can become before anyone realises it, a fortress of reaction. To concentrate exclusive power over some important phase of animal breeding in a single institution, such as a government department, a centralised pedigree registry, or a national artificial insemination service, could be an error of judgment.

There have, however, been agriculturalists who were outstanding in the history of plant and animal production and the present is no exception. All research institutes are familiar with the practical man who follows closely on the heels of research workers and is sometimes ahead of them in applying their ideas. Such men are known to be influential in guiding the thoughts and actions of fellow farmers, and it would probably be advisable to encourage them by making technical assistance more readily available.

and Oeser (1964) have made an interesting study of the way in which Australian farmers develop their conceptual range. They believe that the adoption by a farmer of a new practice he has heard of depends on (a) understanding, (b) accepting its relevance, and (c) deciding whether or not to adopt it. Among Australian farmers, the attitude to knowledge was different from that of town dwellers. Thinking, reading and planning were not thought of by farmers as work. Knowledge achieved by practical experience or personal communication was valued more than book-learning or ideas tested remotely by others. The investigation showed further that readiness to read about and absorb new scientific ideas, and to adopt new practices was positively correlated with skill in coordinating and planning, suitable environmental opportunities, and an unbiased outlook on information. Where a topic is ill-defined (such as "science", or "improvement", without specific definition) individual judgments tend to be vague and much subject to the influence of those with prestige. Consequently, it is natural that a traditionalist group of leaders in a farming community will encourage the rejection of a new idea because they are anchored to their traditional views. Progressives, on the contrary, tend to be wedded to the mobile concept of progressive farming. Although not exactly a surprise, this finding has its interest in the present context. When the adaptability of breed associations, the likelihood of new breeding organisations, and the performance of producer co-operatives is being assessed, the behaviour patterns of elected representatives of farmers and breeders are very pertinent.

Farming is an occupation pursued by men of great variety of age, temperament and circumstance. They cannot be characterised in a word; yet to them decision-taking is an almost hourly occurrence. To a particular challenge, farmers will react at different speeds and in different ways An interesting survey has been made in New Zealand of the reasons why farmers did not adopt herd testing and artificial insemination (Table 10.1). There, artificial insemination, after a late and slow start taking about four years, experienced a rapid expansion for nine years, at the end of which time rather more than one-third of all cows were artificially inseminated During the last three years, the rate of growth has become much slower. Herd testing has a comparatively long history of over forty years and covers about one-quarter of all cows. In New Zealand, as elsewhere, the value of herd-testing depends heavily on the attitudes of mind of farmers who test and on their willingness to apply the lessons learned from the figures. Artificial insemination is similarly affected, although in New Zealand the evidence that it can raise yields is clearer than in most other countries (see

Table 6 2) On the basis of the rather small samples obtained from one area, it would not be wise to place much trust in the details of Table 10 1, but they will serve well as illustrations

TABLE 10 1

Reasons for not using dairy herd testing and artificial insemination given by New Zealand dairy farmers (from New Zealand Dairy Production and Marketing Board, 1964)

Reason	In % Herd testing	Artificial insemination
Not interested in increasing butter fat production	12	14
Not rearing replacements	6	8
No scope for culling	12	—
Testing a nuisance	16	—
A I stock or C R not good enough	—	10
Likes to select own bulls	—	28
Expense	34	22
Apathetic	5	7
Sundry	15	11
Number of farmers surveyed	215	140

In a country which encourages its agriculture, which showed an increase in average herd size (in herds over ten cows) from fifty three to seventy cows in the last ten years, and which has increased butterfat production per cow by about 20 lb a year in the same period, it is significant that such a high proportion of farmers remain unimpressed by the two main improvement techniques In Holland and the Scandinavian countries the proportion is much smaller, but in Britain and the United States it is about the same as in New Zealand

It is instructive to compare these New Zealand observations with the analysis Florence (1964) gives of the motives he thinks might prompt the owner of a business or his salaried manager to decide for or against enlarging the business (Table 10 2) Mixed though they may be, they are sufficiently diverse to guarantee that opportunities will not be grasped with equal fervour by everyone What the owners of pedigree herds will do when faced with the option of expanding operations, submerging themselves in co operatives, or becoming agents of large firms, will vary in a manner hinted at by Tables 10 1 and 10 2 What

the executives of establishments that are already large will do to exploit further opportunities will likewise vary. At one extreme may be those who are young and energetic enough to think on an international scale; at the other extreme are those who will be happy just to retain their posts

TABLE 10.2

Motives for and against expanding the size of business (adapted from Florence, 1964)

	Entrepreneur		Salaried manager	
Motive	for	against	for	against
		Economic		
Cash	Greater profits	Profit not greater	Bigger job	No personal gain
Real cost		Cannot be bothered Tax burden		Expansion might fail
		Psychological		
Power	Empire building	Dependence on outside funds	Power seeking	Fear of others' power
Hobby	Love of work	Pre-occupied with other work	Love of work	
		Sociological		
Fame	Prestige	Preference for amateur status	Prestige of belonging to the business	Professional loyalty
A logical		Own money to play with		No initiative

within which animal breeding will have to work. New institutions of their designing are growing out of the ruins of the old. The pace is set by those who, fascinated by growth, are determined to make a profit and will serve no other cause. Such men are to be found in the poultry and artificial insemination industries. Few of them have arisen through farming organisations, for the qualities they display are not the same as those required for democratic leadership in farming or politics.

The prehistoric distinction between nomadic herdsman and settled agriculturalist can still be traced in the behaviour patterns of the stockman and the grower of crops when confronted with change. Animals are an extension of self for the stockman in a way impossible for less directly responsive plants. But the surviving traces are disappearing, as the arts of animal husbandry give way to the techniques of mass production. The livestock breeders who aim to secure for themselves a share in the ownership and management of large breeding enterprises will have to adapt themselves accordingly. They cannot remain livestock breeders in the usual sense of this phrase.

VIII. Scientists as Decision-makers

Scientists cannot escape decision-making: they decide on problems to study, experimental design, data to collect, and interpretations to accept. Since every true decision, as distinct from an inference, involves an element of choice, the constraint imposed by logic and mathematics rules out, according to Cowan (1963), the study of creative decisions. In spite of the fact, however, that the sources of creative impulses such as desire for knowledge, inspiration and faith are but poorly understood, their practical consequences are evident enough.

Although formerly pursued largely as a cultural activity with the aim of revealing and contemplating the truth, science has become for the most part an unabashed striving for mastery over nature. The great edifice of knowledge has been built mainly to prosecute war, defeat disease, prolong life, and produce more of life's necessities and amenities. In the course of events, scientists may have become personally involved (much as Professor Higgins in Shaw's "Pygmalion"). They will now have to learn to carry ever-increasing responsibility for their decisions, as those who participated in the creation of the atomic bombs became fully aware.

Scientists must be judged less by their intellectual or physical equipment than by the effectiveness of their actions in discovering or applying knowledge (Cox, 1964). There are no pre-ordained ways of making discoveries. If, in the same sense, decision-makers heading a

breeding enterprise are to be judged by results, there must be some acknowledged aims. But, to be sure of progress, the methods must be chosen imaginatively and applied skilfully as in successful art.

Yet, organised science in the shape of scientific societies and research councils has not been notable for enterprise (Welsh, 1965). It has, in fact, turned out to be the function of politicians, a few controllers of firms and industrial boards, and occasional farmers to have the courage of their scientists' convictions. As a class, scientists are not power-seekers like politicians, notwithstanding some well-known empire-builders among them. Nevertheless, science and technology, being both a means and an end of public policy, involve all scientists in ambivalent situations. Not unnaturally, some leave themselves open to the suspicion that they are more interested in pursuing a policy for the benefit of science than a scientific policy for the benefit of society.

The stereotype picture of a scientist is of a man driven by curiosity, whose equipment is intelligence, integrity, observation, thinking and creativity. Very few have this equipment developed to a high degree. Most could lay claim, like other human beings, to some degree of ignorance, bias, poor judgment, vanity and snobbery. Few scientists are non-conforming, original thinkers. The outstanding fact about the motivation of scientists according to Price (1965) is the highly competitive quality of their employment so that they must have rather special inducements to enter it in the first place and even more special ones to succeed in it. As he sees it, the 7% annual increase in their numbers comes through a "birth" rate of some 17% and a "death" rate of 10%—rather like a human population in primitive stages of development.

Policy making, even when it concerns science, has its own problems and techniques, of which neither scientists nor economists, as groups, can presume to possess special or exclusive understanding (Mesthene, 1964). Exceptional individuals, whatever their technical labels, may have personal gifts, which enable them to exert moral responsibilities, and to deal with human beings of irrational faith, tradition and prejudice. The pursuit of science does not confer these gifts on all teachers or research workers. Nevertheless when policy-makers have to grapple with problems and arrive at balanced judgments, they disqualify themselves if they do not insist on the participation in the act of policy-making of those who are specially trained in distilling the essence of technical matters, and who understand the implications of scientific knowledge and new discoveries. For this purpose, it is not enough that an administrator should have taken a degree forty years ago, and it is not enough that he should supplement this by occasional acceptable

advice from "experts" on advisory committees, willing to give off-the-cuff answers to complex and important questions. He needs to incorporate outstanding and active scientists in the apparatus of decision-making and insist that their share of executive responsibility is publicly understood.

This is of great importance in problems of research financing. Thus, the machinery of allocation of public funds for research purposes by such agencies as the National Science Foundation and the U.S. Public Health Service is based on decisions made on the advice of panels of practising scientists by administrators, who as a rule are no longer active in the scientific profession. In spite of the increasing budgets that these agencies have, competition for funds is becoming progressively more severe. For instance, in one unpublished example, while the available funds rose 70% in a recent period of three years, the requests for subvention received during the same time more than doubled. Since, as may be seen from Table 8.2, American colleges and universities depend for 75% of their research and development costs on Federal government agencies, it is clear that scientific administrative decisions may come perilously close to determining the course and scope of the science to come. There is no evidence, so far that programme directors of the fund-granting agencies have become dictators, but the possibility is inherent in the situation.

Few scientists have declared themselves in favour of a scientific autocracy, and many are especially wary of what is called "informed scientific opinion." This does not mean that administrators of entirely non-scientific origins and attitudes would be any more acceptable. Geneticists have reason to regret the time lag in the application of their science caused by decision-makers in the livestock industry who, in the light of subsequent events, seem to have over-valued their own untutored opinions.

It is characteristic of recent years throughout much of the world, that concern about participation of scientists in national policies is manifested in all levels of society (Gilpin and Wright, 1964). The use of scientists as advisors to ministries and departments is not at all new. In the United States, the National Academy of Sciences was founded some hundred years ago by President Lincoln to provide the government with scientific advice. In the field of agriculture and animal breeding, government-supported fact-finding and fact-dissemination agencies are also of long standing in the shape of experiment stations, research institutes, extension and advisory services. But scientific advice has been nearly always on the technical level. The scientists, on the one hand, presented their findings for action to government

offices, and, on the other, distributed technical information to farmers and breeders. The notion, however, that scientists should sit in the inner councils of a nation and participate in decision making and policy formulation is much more recent. At the moment, it seems that the extent of this practice depends largely on the political ideas and personalities of high elected officials. It is, however, clear that the existence of high level advisory committees and councils carries no guarantee that proper study will be made of major problems such as priorities for research expenditure, or that the scientists who advise will bear any burden of responsibility for implementing decisions.

There are undoubtedly many scientists who are anxious to contribute their knowledge and wisdom to decision-making. But it must be recognised that natural scientists are sometimes lacking in social tradition, in comprehension of political constraints, and in understanding of the economic facts of life. Many of them are ill-equipped for a role in high-level decision making and allocation of priorities owing to pride in their scientific morality and a distaste for compromises. The accommodation of politics and the restrictions on openness of thought and word necessary in Big Science in industry and government (especially, in military developments) are foreign to them. Nevertheless, there are those who rise superior to these handicaps. It seems that, eventually, a new breed of administrator combining the multifarious talents required in this position will be needed. Just as the ancient Chinese scholar-bureaucrat, the mediaeval viziers and agents, and the Victorian literary dilettanti have served their turn, so, perhaps, in the future, a class of modern technocrats adapted to recent changes in science-based industries will arise. Whether such a breed can be made to order, as the Shorthorn breed of cattle has been, remains to be seen. The problems of shortage of scientific manpower so far as experimenters and teachers are concerned is probably less acute, even in the face of the tremendous increase in these activities, than that of accomplished and dependable decision-makers.

Readers may have some reservations about the scientific bureaucrat as a decision-maker, and may express some apprehension about the extension of Parkinson's Law to science. Nonetheless in the area of animal breeding, rational and scientifically based decision-making on a national and international scale is going to be called for very soon. Indeed, it may become a rather critical issue as to where and what kind of improvement of livestock should be carried out by whom. It is not sufficient to rely on economists, simply because the biological facts are so intimately connected with the decisions to be made. A fuller understanding of the mechanics of animal breeding rather than simple

reliance on technical advice would certainly be needed by managers responsible for plans to be put into effect.

Manifestly, the strong case for harnessing genetics more effectively to livestock production would be weakened by claiming more than could be delivered. There is much more to be learned about genetics and about its interactions with other forces. As an example, the question of control of breeding policy will serve well.

No matter what the respective merits of breeding procedures recommended by geneticists or developed and practised by breeders may be, the assumption that any one system or method is the only right one appears to be too dangerous to accept. Granted, that if in evaluating the operational merits of competing systems of organisation and breeding, one system will appear to be superior, it does not follow that it would be wise to eliminate all other systems.

The amount of information on which any decision can be based is inadequate to provide an answer which will always remain valid. Accepting that a solution now may interfere with, or make it impossible to adopt later another that might have been better still, there is no doubt that one or more of such better ones exist but are unknown today. To adopt a single system does not allow for the adjustability which will be needed for future changes in environment, and the new objectives towards which animal improvement may be directed.

A geneticist might well be more cautious than a pedigree breeder in making claims for his preferred breeding system, but in that case his decision-making would be influenced by considerations difficult to specify exactly and he would be acting as an informed layman. Faced with the common situation in which the breeding population is too small to sustain two or more different breeding policies, the geneticist will not be able to fall back on his theory for guidance. He will know that in r

variety of ways that would ensure a potential for later changes and modifications should they be necessary, and its size would be determined by the optimism or pessimism of the decision-makers.

IX. Group Values

The chief concern of individuals is with the values which they recognise to be the values of the many groups to which they belong (Churchman, 1961). A "group" of people, such as the membership of a breed association, has identifiable actions and objectives and it functions within a certain teleological framework.

If a group of, say, farmers or scientists works towards certain ends and has certain operational theories, its members tend to think in predetermined ways, collect information favourable to its views, interpret observations subjectively, and constitute a vested interest. Heritability is an instance of a concept which is much conditioned by group values set on it, in this case, by population geneticists who know its meaning and implications, its strength and weaknesses.

Group values are like net genotypic values for complex traits in having much variation of individual components of which the resultant is the group value. This need not correspond to the value of any one component. The more the individuals resemble each other, however, the more distinctive the group value. Where there are conflicting views, they destroy each other and the group value is weak and unobtrusive. Within a group, all individuals are not equal and hence group values tend to approximate the values of persuasive or powerful individuals. As such, they are not necessarily correct or beneficial.

The importance of group values, when they are taken in conjunction with personal characteristics, arises from the various kinds of decision-making situations in which breeders and scientists may find themselves. A rough classification can be made following Churchman and using his eight categories (Table 10.3). It is a condensed version which might be described inadequately as an over-simplification. As a first attempt to use this classification will probably show, real people do not fit conformably into it, but it will also make clear that the group values and attitudes of geneticists and breeders may be far more important in decision-making than academic or social distinction.

It is natural that the majority of the present exponents of population genetics should belong to the category ABC. By virtue of their own genotypes and environments, they have chosen for themselves occupations and activities which are essentially deductive and conventional. It follows that the best use which can be made of them is in work

requiring these qualities, namely, development of new breeds and strains by methods in which these workers are expert.

Management and control of large breeding populations has fallen, at various times and places, to. (a) government departments; (b) tycoons in business; (c) boards representing farmers and others; (d) technocrats.

TABLE 10 3

A classification of scientists (after Churchman, 1961)

A—a = conventional —non conventional
B—b = formal, precise—non-formal, less precise
C—c = deductive —inductive

A	B	C	Forecast the unexpected, originality Mathematics
		c	Arbitrary "facts" as prelude to study of implications Science fiction
	b	C	Speculators by profession
		c	Arbitrary "facts" as prelude to study of implications Science fiction
a	B	C	Precise, principled, e g mathematical economics Sparing in invention of principles
		c	Precise formulation of theory and experiment Usefulness a minor consideration
	b	C	Poets Use vague terms, but general and original—common in economics—significant rather than trivial
		c	Generalisers from facts—data collection is primary aim—limited precision and theorising

to provide information. These people are likely to be different in these four categories, although they should, perhaps, not be. Whereas the tycoon is likely to be attracted to type ABC, because it pushes things to logical conclusions or grapples with complex situations by original methods, the technocrat tends to be a strong believer in his own judgment working on data produced by type abc. This type seems likely to commend itself also to boards and government departments whose collective tastes for originality and enterprise are usually rudimentary. To some extent, the selection of "scientists" for service with breeding enterprises is likely to influence the nature of the "facts" on which they operate and, thereby, on their natures and activities. The most effective place for types ABC and abc would appear to be university departments and research institutes where freer rein can be given to originality.

X. State Responsibilities

Whatever the case in socialist countries, in non-socialist states the weighty question of state obligations arises in a variety of forms. Thus, responsibility for conducting or supporting research is an important state function. It has been discussed in some detail in Chapter 8.

Among other responsibilities, there is also advisory or extension work. The more advanced the technology of breeding is, the less significant does this function become, largely because breeders or cooperative breeding enterprises have their own technical staff. Whereas, no doubt, an agricultural advisor could be very helpful to a Scottish mountain sheep breeder, it is fair to say that in the whole of the United States not one extension man capable of improving the genetic operations of the breeders of egg-laying stock could be found. Even in commercial poultry production much extension work both in the United States and in Britain is being taken over by fieldmen for hatcheries as a competitive service.

enforcement of fair trade practices and honest advertising, but even more so, to regulation of disease. In many states it is illegal for breeders and hatcheries to sell chicks from flocks which have not been tested for pullorum disease. This a matter of protecting the producer. There is also the problem of protecting humans from diseases carried by livestock, though this may be of limited concern in breeding operations.

Official regulation of breeding practices is decreasing in some countries and increasing in others, and may be the most controversial of all of the government activities considered. Licensing of males on basis of conformation or the introduction of regionalisation fall into this category. In California at one time, an attempt was made to enforce poultry breeders' participation in federally-operated improvement plans. Indeed, disease-regulating features of such plan did become part of the law, though other aspects (for instance, restriction of use for breeding purposes to cockerels from dams which have laid some minimum number of eggs) were frustrated by an exceedingly strong opposition from free-enterprise-minded breeders.

Afterword

Most citizens pay very little attention to the provenance of their meat, milk and eggs, but there are nevertheless strong links between the consumer and the breeding of the animals the products of which he eats. His influence makes itself felt through his preferences and discriminations among the goods offered. In areas where the standards of living are high, the economic pressure he exerts is towards higher quality and standardisation, the exact meaning of these descriptions being determined locally according to taste. By degrees, therefore, farmers are becoming obliged to try to deliver uniform products through a closer control of breeding and husbandry, and the subsequent grading of output. In less fortunate areas the need for protein from an acceptable and usually conventional source is paramount, and there is less attention to taste, tenderness and fat. Everywhere, however, the consumer is interested in cheapness and therefore in low cost methods of production. Universal aims of breeding and rearing livestock can hardly be defined except possibly in terms of maximum output of protein. Whether this should be a maximum for a unit of land, a unit of labour or a unit of capital investment, will depend on which component is in least supply. Ultimately, perhaps there will be a suitably weighted combination of the three. Where protein deficiency is unknown, breeding aims may be unacceptable over the short term unless they are closely related to quality.

In the last analysis, it is still the consumer, actual or potential, who brings about the use of science to alter any stage of the process of production and distribution. But the consequences hardly ever affect only the consumer. While his food habits are being changed by hygiene, freeze-drying, prepackaging, and other marketing devices, the added complications and skills required for producing and transporting foods tend to favour the more adaptable, the better financed, and the larger farmer or breeder.

Each new concept arising out of research leads to others. It thus gathers impetus, although the freedom of thought which engenders it always encounters opposition, for it is a human trait to resist any change which adversely affects the skills and status of people. As the rate of scientific development accelerates, it is to be expected that more people will become aware that they are not just spectators of agricultural evolution. Animal breeding is everyone's concern. Those most intimately affected are the breeders themselves, their employees, and the producers who depend on them for breeding animals. There are, at one remove, numerous suppliers of goods and services, extension

personnel, journalists, bankers, administrators and research workers. And beyond these are the processors, wholesalers, distributors, retailers and, finally, consumers.

Over most of the world, animal production is firmly rooted in a close, and even personal, relationship of man with his livestock that is the result of an age-long process of reciprocal adjustments. For a century or so, they have been driven unceasingly to make greater demands on each other but society is still not satisfied. In some places there is hunger and in others cheaper products of higher quality are wanted. Each country strives to improve its competitiveness and achieve the economic growth which will finance its social aspirations. Agriculture must make its contribution and it must do so, as always in the past, by exploiting land, labour, capital and brains. Where technical developments have gone far enough, the advantages of scale accrue to animal production just as they do to other industries, but they are almost impossible to realise while maintaining the traditional husbandry that required a farmer to know and care for his animals. Growing along side it, therefore, is a new science-based industry with economic goals that allow of no concessions to sentiment.

This new industry, and to a lesser extent the old one, are at once the creations and the creators of the technology which serves them. Large sums of money have gone into education, research and development for industry. Agriculture has been allotted only a small share, yet enough of it has been expended to provide, among other things, a theoretical basis for breeding the animals that produce meat, milk, wool and eggs, and a set of techniques more effective than those formerly available. Until recently, however, two necessary conditions for the use of the new methods have usually been lacking: the objectives of breeding policy have not been defined in economic terms, and there have been no enterprises large enough to seek them independently of the established system of breeding. As is well-known, one or the other, and, occasionally, both of these conditions are now being met in some countries, so that the process of industrialising animal protein production can be expected to continue and eventually to embrace all forms of livestock.

Once started, the fusion of economic efficiency with technical expertness is likely to continue at a rising pace. Under the circumstances, the attack on traditional methods, wherever they are deemed to be restrictive, has proceeded from matters such as cultivations and herbicides which a farmer may adopt at discretion, to fundamentals such as land tenure, crop rotations and co-operative marketing which are accompanied by legal sanctions against non-conformists. The idea that animal production can be thought of and organised after the manner of factory

production is steadily gaining ground in spite of the fact that it generates a strong opposition from those who are emotionally or financially engaged. It is at least as radical a departure from man's most ancient occupation as the automated production line is from a cottage craft. Where a political balance will be struck between the supporters of traditional methods and the proponents of cheap food no-one can tell. But in view of the growing human population and expanding scientific research, it seems unlikely that any one answer will finally dispose of the problem. As long as agrarian squalor and hunger afflict the world, the cry for more and better food will be heard.

Constructive breeding in future, especially for intensive production in a science-based industry will probably necessitate the subdivision of animal populations into breeding groups of operationally adequate size and a fast service of performance testing and data-processing. These will permit selection aims to be energetically pursued and inferior varieties discarded. Inter- and intra-breed rivalry will be encouraged by regional autonomy (where breeding is organised on a national scale) by adapting breed associations to the techniques of breeding for economic merit, by having performance testing adequate in extent and more effective in method, and by systematic importation Selection will occur not only within herds or flocks but between them and between breeds as it does now. The ultimate goal is the mutual adaptation of genotypes and environments.

The success of a breeding programme can be measured in several ways. In some circumstances the rate of change may be of overriding importance, in others, the kind of change, or the cost of obtaining a unit of change. But whichever is taken as the criterion, the number of breeding animals in a population is of critical importance. It does not follow that control over large numbers, which is necessary for rapid advances from selection of breeding stock, will automatically result in progressive improvement. The other advantages of size will secure its economic future. Auctioneering, artificial insemination and sales promotion sometimes depend heavily on the continued prosperity of the pedigree breeding system. For them, improvement by breeding may well be irrelevant and even a threat to their existence.

Large-scale operations do not have to be modelled exactly on those now becoming characteristic of poultry, but by some means the power of fixing policy and securing action must be concentrated in a few capable hands. How to achieve this, while ensuring that those who wield the power remain accountable for their use of it, is a fundamental social and political question common to most human activities. Put in a form appropriate to animal breeding, the problem is to evolve

policy-making bodies whose activities are consistent with the national or world interest. Without such institutions there can be no acceptable aims of breeding, and without aims there can be no exploitation of the power of science to increase the productivity of the livestock industry through breeding.

Pedigree breeding, as it is commonly understood, has in the past contributed a great deal to livestock production, but it must now expect its services and costs to be critically examined. These costs have to be borne by the industry and ultimately by the consumer, so it is reasonable to ask what services are rendered and what they are worth, questions that commercial enterprises have to ask themselves. Public interest sometimes requires restraint on the pursuit of efficiency. Without going so far as to shield inefficiency absolutely, a country may decide to offer partial or temporary protection, with a view to encouraging an established institution to improve its competitiveness against its rivals. There may also be such a strong public distaste for monopolies that some loss of efficiency is tolerated in order to avoid them. In other situations, the strength and political influence of those who support the existing breeding system may be great enough to suppress the knowledge that it could be improved. An acceptable solution to conflicting views may be found in allowing or encouraging two or more independent breeding organisations that may differ in aims and methods but are subject to performance tests under neutral supervision. This stage has yet to be reached for the larger livestock.

Means of measuring performance need to be constantly developed and refined for the comparison of breeds and crosses and for testing new varieties. Although performance testing of pigs, sheep and cattle is still inadequate, even rudimentary, the remedies lie in a striving for perfection, not in discouragement and the assumption of a superior attitude. There will be no going back to unaided eye judgment. It is easier to imagine international arrangements for testing livestock, especially pigs and dairy cattle in Northern Europe where conditions of husbandry are rather similar.

Making sure that varieties produced abroad can be imported and adequately tested is the best insurance that complacency will not develop in those responsible for breeding. In many countries, there may be little prospect of a government establishing an agency for the express purpose of making available the material from which more advanced biological machines could be developed, yet there is much to be said in its favour. Such an agency would be charged with making available the best livestock, no matter what their origins. Practically all varieties of crops and livestock in Western countries are of imported

origin (and man himself is no exception), but no attempt has yet been made to carry out systematically a process that occurred sporadically in the past. Whether or not this comes to pass, there seems to be a good case for an intelligent policy of importation and testing. Even in the unlikely event of a country having nothing to gain from foreign breeds themselves, importations may provide a stimulus to home breeders. Appropriate veterinary precautions must be taken and some way found of discouraging projects that have little hope of being carried out. This is far from easy, since successful importations have very often been due to breeders prepared to fight for their ideas against the establishment and the orthodox masses. In future, however, the enterprising breeder will often be a large corporation or consortium which is clear about what new genetic material it needs, and is technically equipped to test stocks quickly and adequately.

As the methods of agriculture change and the craftsman gives way to the technician, the nature and financing of research call for re-appraisal. What passes muster in agriculture based on comparatively small farms will not do for a highly competitive economy with big businesses. Intensive production cannot be served in the same way as an extensive pastoral husbandry. But existing arrangements tend inevitably to be better adapted to the more out-of-date or undeveloped aspects of agriculture than to the most intensive and highly capitalised. *Many aspects of this complex activity of a modern society that apply to* animal breeding justify some constructive thinking now. In the past, much effort has been put into studying questions arising in the pursuit of agriculture by farmers and much more into trying to convey the results to them. While this effort still goes on, different research with a high order of urgency is required as a result of the organisational changes in farm industries. Operational problems are seen in far greater financial clarity than before, and it is worth paying much for speedy solutions to them. Slow deliberate attack over a broad front, inadequate facilities for applied and developmental studies and lack of financial incentives to students and research workers of ability create dissatisfaction in an active and progressive industry. Since time is short, it should not be squandered. The horizon of a scientist interested in a basic biological problem may be as much as ten years away, while for another concerned with adapting a new process to industry it may be only one or two, or even less, if the problem is operational in character. As a result, geneticists who are devoted exclusively to research, tend to take a longer view of breeding plans than do breeders pre-occupied with economic survival from year to year. But this incompatibility is becoming academic.

Decision makers responsible for a large enterprise are obliged to address themselves at first to developmental or operational research but as the enterprise grows and they begin to plan for a confident and receding future, basic problems attract more of their attention. Somehow present needs must be balanced against long-term hopes. For a business which has to finance research out of profits, there are several factors that determine what is spent. The size of the business and its financial strength exert a weighty influence, and so does the stimulus provided by powerful and aggressive competitors. How much the research programme will cost and what advantages it will confer on the marketing of the product are questions that have to be answered no matter how awkward they are. When the temperaments of research workers, their interests, qualifications, and age are added to this fluid situation, the public and private supporters and administrators of research in agriculture are saddled with a task which can be neither neglected nor finally accomplished. How much to invest in livestock improvement is, however, a question that is not susceptible of an exact answer by any kind of decision maker. Added to the genetic uncertainties about achievable rates of progress, there are economic and psychological imponderables that influence enthusiasm and willingness to take risks or mortgage the future. No rigid or doctrinaire attitudes can be supported when the justifiable investment can rise or fall with time or from one class of stock to another. This applies with as much force to the pedigree system as to any other method of breeding an elite population, for in the last resort the incidental costs and profits of all methods must be met by someone. Unless there is a change for the better in the genetic and economic merit of each breed, it is difficult to see how any outlays on breeding for improvement can bring returns to the ultimate financial source. Constructive breeding therefore must have positive aims, anticipate the future correctly, and temper the rigours of genetic theory with a proper regard for costs and returns.

Animal genetics stands ready to help in reaching the objectives of society. It is for society to decide where its ambitions lie and what are its purposes If there is nothing so important as the production of foods to allay hunger, mitigate poverty, or support luxury, there is no-one more important than producers. The economic goals of agriculture are paramount. Institutions are devised that will bring them closer, and men are made to fit the institutions. Like many other sciences, genetics has been nourished mainly in Western countries where orthodox economic theory shelters public apathy and bureaucratic indifference to the hastening ills of mankind. Accordingly geneticists can apply themselves without moral distinctions to improving the poor man's pig,

or the rich man's conspicuous beef. They have also long known that the power of their science can be frustrated by vested interest and a distaste for controversy. Individualism flourishes, and old habits die hard, the spectre of overpopulation notwithstanding. In time, society may be obliged to become more explicit about its purposes. When that day comes, it may be easier to define how science can best contribute to the quality of life of all the earth's inhabitants.

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